Fall 2018

Small mammal community dynamics and the dispersal of mycorrhizal fungi

Ryan B. Stephens
University of New Hampshire, Durham

SMALL MAMMAL COMMUNITY DYNAMICS AND THE DISPERSAL OF MYCORRHIZAL FUNGI

BY

RYAN B. STEPHENS

Baccalaureate Degree (BS), University of Wisconsin - Stevens Point, 2009

Master's Degree (Natural Resources), University of Wisconsin - Stevens Point, 2012

DISSERTATION

Submitted to the University of New Hampshire

in Partial Fulfillment of

the Requirements for the Degree of

Doctor of Philosophy

in

Natural Resources & Earth System Sciences

September, 2018

This dissertation has been examined and approved in partial fulfillment of the requirements for the degree of:

Doctor in Philosophy in Natural Resources & Earth Systems Science by:

Dissertation Director, Rebecca J. Rowe
Associate Professor of Natural Resources & the Environment
University of New Hampshire

Erik A. Hobbie
Research Professor/Affiliate Professor of Earth Systems Research Center
University of New Hampshire

Mark J. Ducey
Professor of Natural Resources & the Environment
University of New Hampshire

Daniel J. Hocking
Assistant Professor of Biology
Frostburg State University

Thomas D. Lee
Associate Professor of Natural Resources & the Environment
University of New Hampshire

Mariko Yamasaki
Research Wildlife Biologist/Team Leader
USDA Forest Service Northern Research Station

On May 18, 2018

Original approval signatures are on file with the University of New Hampshire Graduate School

ACKNOWLEDGEMENTS

When I first started my dissertation in the fall of 2012 I could have never imagined the journey it would take me on. As my research interests have diversified, so have the paths I've traveled and the people that I have interacted with. Herein I'd like to thank those that have helped to shape this research path. First and foremost I thank my advisor, Rebecca Rowe, for her constant encouragement and flexibility over the past six years. She has pushed me to think broadly and to stay focused (any deviations are of my own accord). I have also had the good fortune to have five other committee members that are both an amazing group of scientists and people. Mark Ducey has been integral in helping to design a protocol to sample and analyze truffle abundance and I have learned much about how forests grow and function from his classes. Erik Hobbie has contributed immensely to isotopic analyses and I appreciate his enthusiasm and support toward the mycophagy portion of my research. Early on in my dissertation work, Dan Hocking helped immensely with statistics, R code, and general grad school questions. Tom Lee's community ecology course opened my eyes to the broad field of community ecology and, more importantly, the history and theory surrounding it. Finally, without Mariko Yamasaki's encouragement and support none of the field work for this project would have been possible.

My dissertation draws on data collected both in the field and lab, and I am grateful to have had the help of numerous undergraduates who have made this project possible. In particular, Chris Burke, Tyler Remick, Andrew Uccello, Lily Poland, and Marissa Cyr all survived one or more field seasons. I am especially grateful for Tyler's diligent efforts with the truffle surveys and processing and sorting literally thousands of truffles. Microscopy of small mammal scat took over two years to complete and without the help of Matt Wilson, Andrew Uccello, Tyler Remick, and Marissa Cyr I would still be looking through the microscope today.

Stephanie Smith, Corina Danielson, and Johnny Nowick prepared hundreds of hair samples and potential food sources for isotopic analysis.

I would also like to thank all those who have helped me along my journey. When I first started my dissertation I did not know what a truffle was. Danial Luoma was instrumental in helping me to figure out the tools and techniques needed for truffle sampling. James Trappe and Michael Castellano generously contributed their time to help identify truffles collected in the field and spores detected in scat samples. When truffle sampling extended into the fall of 2014, a number of people stepped up to help make this possible including: Karrah Kwasnik, Brooks Kohli, Bianca Rodriguez Cardona, Alena Warren, Tyler Mahard, Kristen Stearns, Cortney Woelfl, Alex White, and Mark Messina. Andy Ouimette of the UNH Stable Isotope Lab processed all of the samples used for isotopic analyses. Franz Lichtner and Melissa Knorr freeze dried the rodent scat samples. I would like to thank Chris Costello for all her support while we stayed at the Bartlett Experimental Forest field station. My lab mates, particularly Brooks Kohli, provided lively discussions and helpful feedback along with way. My parents have been most supportive in all aspects of my life as I worked on my dissertation and I thank them greatly. Finally, I would like to thank my wife, Karrah Kwasnik, for all her support over the last five years. Not only did she take several weekends to dig for truffles ("which is only fun for the first two hours"), but has helped to make graphs, edit personal statements for grants, and has listened to numerous practice presentations ("which are generally not great'') . Moreover, she has consistently sacrificed her time to make dinner and do other errands so I could write or reach looming deadlines. I am forever indebted.

Funding to support my research was provided by the New Hampshire Agricultural Experiment Station as part of the USDA National Institute of Food and Agriculture McIntire-

Stennis Project (0229197 & 1006881). Further support was provided by the University of New Hampshire NRESS Student Support Fund, the American Society of Mammalogists: Grants in Aid of Research, North American Truffling Society, and the Mycological Society of America: Forest Fungal Ecology Research Award. I am also grateful to the UNH graduate school for a Summer Teaching Assistant Fellowship and UNH Dissertation Year Fellowship that supported me during my final year.

TABLE OF CONTENTS

Acknowledgements ..... **iii**

List of tables ..... **viii**

List of Figures ..... **x**

Abstract ..... **xv**

Chapter 1 ..... **1**

Synchrony in small mammal community dynamics across a forested landscape[1] **1**

Abstract 1

Introduction 2

Methods 4

Results 14

Discussion 18

Chapter 2 ..... **32**

Drivers of truffle biomass, community composition, and richness among forest types in the northeastern US[2] **32**

Abstract 32

Introduction 33

Methods 35

Results 43

Discussion 48

Chapter 3 ..... **64**

Pulsed resource availability changes dietary niche breadth and partitioning between generalist rodent consumers[3] **64**

Abstract 64

Introduction 65

Methods 66

Results 75

Discussion 76

Chapter 4 ..... **86**

The underappreciated role of generalists in rodent-mycorrhizal dispersal networks[4] **86**

Abstract 86
Introduction 87
Methods 90
Results 98
Discussion 101
Literature Cited 114
Appendix A 130
IACUC Approval for use of Animals in Research 130
Appendix B 133
Supplementary Figures for Chapter 1 133
Appendix C 135
Supplementary Tables and Figures for Chapter 2 135
Appendix D 137
Supplementary Materials for Chapter 3 137
Appendix E 139
Supplementary Material, Tables, and Figures for Chapter 4 139

LIST OF TABLES

Table 1.1. Captures of 22 small mammal species from 3 years of sampling in the White Mountains National Forest, New Hampshire and Maine. A total of 108 sites were surveyed, with 36 sites trapped each year. Order is based on the rank abundance of the three-year total. Abundance analyses were conducted for species in boldface type..... 24

Table 1.2. PERMANOVA analysis showing the effect of year and physiographic characteristics on small mammal community composition across 108 sites. Distance among small mammal communities is based on a Bray Curtis dissimilarity matrix generated from detection-corrected abundances for the 15 most common species. We applied repeated measures by using site as the nesting factor..... 25

Table 1.3. Results of Mantel tests comparing small mammal community similarity (Bray Curtis) and linear distance (km). Significance of Mantel tests was based on 999 permutations..... 26

Table 2.1. Total number and frequency (percent of 4-m^2 plots with ≥ 1 sporocarp) of truffle and mushroom sporocarps across forest types from field surveys. Number of plots sampled was 256 in each forest type for a total of 768 plots across all forest types. Taxa are arranged from most abundant to least abundant and those with the same total number are arranged alphabetically by genus. Number and frequency were calculated separately for truffles and mushrooms. 56

Table 2.2. Percent of eastern chipmunk scat samples containing truffle and mushroom sporocarps across forest types. Taxa are arranged from most abundant to least abundant and those with the same total number are arranged alphabetically by genus. 57

Table 2.3. Best mixed effects models for predicting species-specific truffle and mushroom biomass (biomass of *Elaphomyces* spp. were log transformed). Coefficients for predictor variables and their associated standard error are shown under fixed effects. Standard error due to grid, station, and residual are shown under random effects. Note that residual standard error varies by forest type. Terms included in the model are considered important based on AIC scores from backward model selection. Basal area of balsam fir, basal area of beech, distance to stream, and slope were not important predictors for any species and were not included in the table..... 58

Table 2.4. Results of multiple regression analyses showing the effects of forest type and time on truffle richness from field surveys and eastern chipmunk scat. The effect of mixed and softwood forest is relative to hardwood forest. Bolded *P*-values denote statistically significant variables at $\alpha = 0.05$. 59

Table 3.1. Optimal mixed effects models predicting $\delta^{15}N$ and $\delta^{13}C$ values from *P. leucopus* and *P. maniculatus* hair samples. Fixed effects variables included species (*P. leucopus* and *P. maniculatus*), season (summer and fall), masting phase (masting and non-masting), and forest type (hardwood, mixed, and softwood). For each variable, the effect is relative to the one not

listed (e.g., effect of *P. maniculatus* is relative to *P. leucopus*). Random intercept includes year and grid for $\delta^{15}N$ and year for $\delta^{13}C$. Both $\delta^{15}N$ and $\delta^{13}C$ models have a residual standard error structure that varies by masting phase. Bolded *P* values denote statistically significant variables at $\alpha < 0.10$. 81

LIST OF FIGURES

Figure 1.1. Distribution of sampling sites during the summers of 1995, 1996, and 1997 in the White Mountain National Forest, New Hampshire and Maine. In each year, 18 sites were trapped with snap trap grids and 18 with pitfall trap arrays. Snap trap grids consisted of 75 Victor snap traps and 25 Museum special snap traps. Pitfall arrays consisted of 10 -2.8 L pitfall traps arranged along three drift fences (see inset). 27

Figure 1.2. Results of an open population hierarchical model analyzed within a Bayesian framework for the 15 most abundant small mammal species. Species were modeled separately and are arranged from top to bottom in order of descending modeled abundance for 1995. Shrews are indicated in boldface type. Detection variables are indicated by (*p*). Circles indicate mean response in abundance or detection and error bars represent 95% credible confidence intervals. Closed circles indicate parameters for a species that do not contain zero within 95% credible intervals. The effect of hardwood and mixed forest is relative to softwood forest and the effect of 1996 and 1997 are relative to 1995. Positive values for trap type indicate an increased response to snap trap whereas negative values indicate an increased response to pitfall traps. ... 28

Figure 1.3. Mean site abundance as calculated from detection corrected abundance estimates for the 15 most common small mammal species at 108 sites in the White Mountain National Forest, New Hampshire and Maine. Plots are arranged by forest type: hardwood (top), mixed (middle), and softwood (bottom). Circles represent mean abundance for a given year and bars indicate 95% confidence intervals. Species are arranged from left to right in order of descending modeled abundance during 1995. Shrews are indicated in boldface type. 29

Figure 1.4. Box-and-whisker diagrams of four community metrics (abundance, richness, diversity, and evenness) for small mammals in hardwood, mixed, and softwood forests during each of the three survey years. Capital letters denote significant differences of a metric across years within a forest type based on Friedman tests and pairwise Wilcox tests, and lowercase letters denote significant differences between habitats within a year based on Kruskal-Wallis tests and pairwise Wilcox tests (only indicated for years with significant differences). Boxes with the same letters are not significantly different, whereas different letters indicate a significant difference. Corresponding test statistics for Friedman tests and Kruskal-Wallis tests can be found in Table B1 and B2, respectively of Appendix B. 30

Figure 1.5. Similarity among small communities by forest type and year. Panels (A) and (B) are a two-dimensional nonmetric multidimensional scaling ordination of the 108 sampling sites over the 3 sampling years (324 total communities). Increased pairwise distance between sites (circles) indicates decreased similarity of community composition. Overlays represent small mammal

community relationships with year (A) and forest type (B). The relative spread of sites within these categories can loosely be interpreted as the degree of community concordance. Outlined circles (A) represent communities composed of abundance data from sites which were trapped in that year, whereas circles without an outline represent communities composed of model predicted species abundance data (i.e., sites were not trapped in that year and species abundance data were predicted based on landscape variables, detection variables, count data from other sites trapped during that year, and count data from the year it was trapped). Panel (C) is a heat diagram of pairwise Bray Curtis similarity values (where 0 = completely dissimilar and 1 = identical) between forest types and years. Larger numbers and lighter colors indicate more similar communities. Abbreviations refer to forest type: Hard (hardwood, n = 39), Mixed (mixed, n = 40), and Soft (softwood, n = 29). 31

Figure 2.1. Location of grids used to sample sporocarps and eastern chipmunks at Bartlett Experimental Forest, New Hampshire, USA (A, D). A total of 12 grids consisting of an 8 x 8 station arrangement (64 total stations) was stratified across hardwood (n = 4), mixed (n = 4), and softwood (n = 4) forests (D, E). Within each of the eight grid columns, two stations were randomly selected for a total of 16 stations for sporocarp surveys (E). From each of these 16 stations, four sporocarp sampling plots were established in cardinal directions 2 m from the station center and one randomly sampled in June, July, August, or September/early October for a total of 64 plots sampled per grid and 768 plots across all grids (F, C). Eastern chipmunks were trapped on each grid with Sherman live traps set at each of the 64 stations in June, July, and August. Scat samples were collected from individual chipmunks upon first capture within a month for a total of 167 scat samples (B). 60

Figure 2.2. Comparison of the occurrence and relative abundance of the six most common truffle species observed in field surveys (left, n = 768) and spores in eastern chipmunk scat samples (right, n = 167). Sporocarps were collected from June through early October and scat was collected from June through mid-August. Stage of sporocarps refers to no spore formation in gleba (unripened), asci formed but many spores not mature (ripening), spores mature (mature). Sporocarp density was calculated by pooling the number of each stage within a species across a grid and standardizing to a 100 m2 area. 61

Figure 2.3. Mean biomass (kg/ha) of total truffle standing-crop, total mushroom standing-crop, and the six most common truffle species among hardwood (H), mixed (M), and softwood (S) forest types from field surveys. Bars indicate standard error. Species are arranged from the most abundant on the upper left to the least abundant on the bottom right. Within taxa, forest types sharing a common letter were not significantly different ($P < 0.05$) as indicated by mixed effects models and Tukey's post hoc tests using log transformed biomass data. 62

Figure 2.4. Richness of truffle spores in eastern chipmunk scat samples from June through mid-August (A), richness of truffle species fruiting from field surveys (B), and a two-dimensional

nonmetric multidimensional scaling (NMDS) ordination of truffle communities based on sporocarp abundance from field surveys (C). Fitted vectors of the environmental variables indicate the direction (increasing) of the environmental gradient with length proportional to correlation with the NMDS ordination. Only significant (envfit, $P < 0.05$) environmental variables are shown: basal area of white ash (Ash), basal area of American beech (Beech), basal area of eastern hemlock (Hemlock), leaf litter depth (Litter), basal area of red maple (Maple), and basal area of red spruce (Spruce). Corresponding envfit statistics can be found in Table C1 of Appendix C. For both sporocarp richness and the NMDS ordination, sporocarps were aggregated at the grid level within a sampling period. The corresponding multiple regression analyses showing the effects of forest type and time on truffle fruiting richness based on scat (A) and field surveys (B) are shown in Table 2.4. 63

Figure 3.1. Contrasting predictions for changes in niche breadth (A) and overlap (B) based on optimal foraging theory (solid line; C) and competition theory (dashed line; D) during low resource availability (non-masting) and high resource availability (masting). Under optimal foraging theory, intraspecific niche breadth is highest during non-masting (A, C) and interspecific niche overlap for *Peromyscus leucopus* (PELE) and *P. maniculatus* (PEMA) should not differ between non-masting and masting (B, C). Under competition theory, intraspecific niche breadth and interspecific niche overlap are predicted to be lowest during non-masting and highest during masting (A, B, D). 82

Figure 3.2. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of major food sources for *Peromyscus leucopus* and *P. maniculatus* (A). Small shapes indicate sample values (analyzed individually for EM and AM fungi and aggregated at the grid level for other food sources) and large shapes with bars indicate means and standard deviation of $\delta^{15}N$ and $\delta^{13}C$, respectively: beech nuts (1.0 ± 0.6; -22.5 ± 0.8‰; $n = 6$), red maple seeds (-1.3 ± 0.5‰; -20.8 ± 0.4‰; $n = 12$), ectomycorrhizal (EM) fungal sporocarps (8.0 ± 2.3‰; -22.6 ± 0.9‰; $n = 56$), arbuscular mycorrhizal (AM) fungal sporocarps (1.9 ± 0.6‰; -21.8 ± 1.4‰; $n = 5$), berries (1.6 ± 1.9‰; -29.2 ± 1.1; $n = 10$), and arthropods (5.8 ± 1.3; -20.7 ± 0.7‰; $n = 12$). Values of $\delta^{15}N$ and $\delta^{13}C$ have been adjusted by +1.92 and +4.64, respectively, to correct for dietary enrichment; putting food sources into the isotopic space of consumer hair. Boxes and numbers indicate the number of weeks that a food source is available during the summer and fall hair growing period (B). For beech, solid boxes and white numbers indicate the number of weeks available during a masting event and dotted boxes and black numbers indicate availability during a non-masting event. 83

Figure 3.3. Biplots of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes (Left) and results of mixing models showing the proportion of food items contributing to the diets of *Peromyscus leucopus* and *P. maniculatus* (Right) during beech masting and non-masting phases. Circles represent hair samples of individuals (*P. leucopus* = filled; *P. maniculatus* = open) and ellipses represent the standard ellipse area corrected for small sample size (SEA_c). Medians of dietary proportions are indicated by a thick horizontal bar and Bayesian credible intervals are denoted by

box width (50% thick box; 75% intermediate box; and 95% thin box). Sample sizes for *Peromyscus leucopus* and *P. maniculatus*, respectively are: summer 2014 (59, 63), fall 2014 (24, 45), summer 2015 (53, 37), and fall 2015 (39, 44). 84

Figure 3.4. Bayesian standard ellipse area (SEA_B) (Top) and overlap (Bottom) for *Peromyscus leucopus* and *P. maniculatus* during the masting and non-masting periods. Medians are indicated by the thick horizontal bar and Bayesian credible intervals are denoted by box width (50% thick box; 75% intermediate box; and 95% thin box). Different letters between seasons indicate that the probability is > 0.90 that the larger group is greater than the smaller group. 85

Figure 4.1. Consumption of fungi by rodent species. (a) Percent of fungi in the diet of rodent species as indicated by Bayesian mixing models, (b) taxon richness of fungal spores in scat, and (c) diversity of the fungal spore community in scat . Medians of fungal proportions are indicated by a thick horizontal bar and Bayesian credible intervals are denoted by box width (50% thick box; 75% intermediate box; and 95% thin box). Boxplots of richness are based on individual fungal taxa in scat and boxplots of diversity are the Shannon diversity index based on the abundance of spores after relativizing across all scat samples for each fungal taxa. Mixed effects models with Tukey's post tests were used to test for differences in richness and diversity among rodent species. Rodents with the same letters are not significantly different, whereas years with the same letters are significant different. Statistics for mixed effects models for spore richness and diversity can be found in Table E3 of Appendix E. 107

Figure 4.2. Boxplots of rodent abundance among forest types and years. For each rodent species, mixed effects models with Tukey's post tests were used to determine differences in abundance among years and forest types. Within a forest type, years with the same letters are not significantly different, whereas years with the same letters are significant different. For *Myodes gapperi*, lines above bars connect forest types with significantly different abundances within a year. No other rodent species showed significant differences among forest types. Statistics for mixed effects models can be found in Table E5 of Appendix E. 108

Figure 4.3. Relationship between abundance and species strength for rodents in incidence networks (top row) and disperser importance networks (bottom row). Pearson's correlations are shown in the upper right hand corner. All correlations were statistically significant ($P < 0.001$). Dashed line indicates a 1:1 relationship and is provided for reference. 109

Figure 4.4. Dynamics of incidence and disperser importance networks among forest types and years. Within a year, networks are based on the averages of four replicate trapping grids for each forest type, with the exception of hardwood and softwood forest types in 2013 that are based off of three replicates. Fungal taxa are indicated by letters and rodent species by four letter genus/species abbreviations (see below). For all networks, fungal taxa are standardized whereas the length of the bar for rodents represents their relative contribution to mycorrhizal dispersal.

For a given fungal taxa, dark gray bars above letters denote average number of interactions with all rodent species in incidence networks and average number of spores carried by all rodent species in disperser importance networks. Dashed lines at far left side of bars denote 12 interaction and 50 million spores for incidence and disperser importance networks, respectively. Fungal taxa abbreviations: A (*Glomus*), B (*Elaphomyces verruculosus*), C (*Elaphomyces macrosporus*), D (*Elaphomyces bartlettii*), E (Russulaceae 1), F (Unknown 1), G (Boletaceae 1), H (Russulaceae 3), I (*Hydnotrya cubispora*), J (*Elaphomyces americanus*), K (*Octaviania*), L (*Cortinarius*), M (Unknown 2), N (Russulaceae 2), O (*Elaphomyces oreoides*), P (*Gauteria*), Q (*Endogone pisiformis*), R (*Hydnobolites*), S (*Rhizopogon*), T (Boletaceae 2), U (*Entoloma*), V (*Hydnotrya tulasnei*), W (*Hysterangium* spp. 3), X (*Leucogaster*), Y (*Melanogaster*), Z (*Tuber*), a (*Hysterangium* spp. 2), b (*Genea*), c (*Gymnomyces*), d (*Leucophleps*), e (*Hymenogaster*), f (*Hysterangium* spp. 1), g (*Chamonixia*), and h (*Elaphomyces remickii*). Rodent abbreviations: MYGA (*Myodes gapperi*), NAIN (*Napaeozapus insignis*), TAST (*Tamias striatus*), PEMA (*Peromyscus maniculatus*), and PELE (*Peromyscus leucopus*). 111

Figure 4.5. Boxplots indicating species strength of the five rodents in disperser importance networks. Within a given year and forest type, significant differences were determined with a ANOVA: 2013 Hardwood ($F_{4,10} = 2.23$; $P = 0.138$), 2014 Hardwood ($F_{4,15} = 6.21$; $P = 0.004$), 2015 Hardwood ($F_{4,15} = 6.21$; $P = 0.272$), 2013 Mixed ($F_{4,15} = 8.66$; $P < 0.001$), 2014 Mixed ($F_{4,15} = 13.43$; $P < 0.001$), 2015 Mixed ($F_{4,15} = 0.85$; $P = 0.518$), 2013 Softwood ($F_{4,10} = 10.33$; $P = 0.001$), 2014 Softwood ($F_{4,15} = 6.71$; $P = 0.003$), and 2014 Softwood ($F_{4,15} = 4.54$; $P = 0.013$). Rodents with the same letters are not significantly different, whereas rodents with different letters are significantly different. 112

Figure 4.6. Boxplots of network-level metrics for incidence networks (white) and disperser importance networks (gray). For each metric, mixed effects models with Tukey's post hoc tests were used to test for differences among years and between network types. Within a network type, years with the same letters (lower case for incidence networks and upper case for disperser networks) are not significantly different, whereas years with different letters are significant different. Within a year, an asterisk denotes significant differences between network types. Statistics for mixed effects models can be found in Table E6 of Appendix E. 113

ABSTRACT

SMALL MAMMAL COMMUNITY DYNAMICS AND THE DISPERSAL OF MYCORRHIZAL FUNGI

By

Ryan B. Stephens

University of New Hampshire, September, 2018

Animals are an integral component to forests, yet few studies have examined the direct and indirect effects of their resource use on ecosystem function. The mutualistic interactions between small mammals and truffles offers an excellent opportunity to investigate how animals contribute to ecosystem function. Truffles, the spore-bearing fruiting bodies of mycorrhizal fungi, are consumed by forest-dwelling small mammals. Mycorrhizal fungi are symbiotic with trees, colonizing roots and increasing the tree's ability to take up nutrients. Because mycorrhizal fungi are extremely limited in their ability to disperse, small mammals play a critical role in forests by consuming truffles and dispersing their mycorrhizal spores. However, little is known about the factors that contribute to truffle consumption and subsequent spore dispersal by small mammals.

I investigated small mammal (rodents and shrews) community dynamics and truffle diversity in New England and explored how competition and habitat specificity interacted with resource availability to shape small mammal diets and spore dispersal capacity. In Chapter 1, to

determine the impact of species population fluctuations on community dynamics, I analyzed a USFS dataset on small mammal occurrence and abundance collected over a three-year period in the White Mountain National Forest (WMNF). I found that population fluctuations were synchronized among species, creating high within year concordance in community dynamics in the region (independent of forest type), and low among year similarity in communities. In Chapter 2, to better understand truffle diversity, environmental associations, and phenology, I conducted detailed truffle surveys among forest types at Bartlett Experimental Forest (within the WMNF region). I also contrasted field survey data with those derived from the truffle spores contained in scat samples of a widespread generalist, the eastern chipmunk (*Tamias striatus*). I found that truffle biomass was 10 times higher in softwood than hardwood forest and that richness of fruiting truffles increased over the summer. Basal area of eastern hemlock (*Tsuga canadensis*; a tree species in regional decline) was the primary driver of truffle biomass and community composition.

To explore how resource availability shapes dietary niches among small mammal species and contributes to mycorrhizal spore dispersal, I trapped small mammals in hardwood, mixed, and softwood forest at Bartlett Experimental Forest over a three-year period. During this time, natural pulses of mast-fruiting of American beech (*Fagus grandifolia*) created variable levels of beech nut availability (a high quality food resource). In Chapter 3, I focused on two congener rodent species (white-footed mouse [*Peromyscus leucopus*] and deer mouse [*P. maniculatus*]), both of which are generalist consumers. I reconstructed their diets seasonally using stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) of hair and measured both intraspecific dietary niche breadth and interspecific niche overlap. Changes in niche breadth were generally consistent with predictions of optimal foraging theory, with both species consuming more beech nuts, less fungi, and having

a narrower niche breadth during masting seasons compared to non-masting seasons. In contrast, changes in niche overlap were consistent with competition theory, with higher niche overlap during masting seasons than during non-masting seasons. In Chapter 4, I used microscopy of scat and network analyses to determine how population fluctuations, diet, and resource availability interact to shape mycorrhizal dispersal by small mammals. The southern red-backed vole (*Myodes gapperi*), a fungal specialist, carried a more diverse spore community than rodent generalists and was consistently the most important disperser in its favored habitat (softwood forest where truffle abundance was high). Nevertheless, during years when generalist species such as *T. striatus* and *P. maniculatus* reached high abundance (following beech masting) their relative importance in networks was equal to or greater than that of *M. gapperi*, particularly in hardwood and mixed forest where *M. gapperi* was less common. These findings suggest that although fungal specialists play key roles in rodent-mycorrhizal dispersal networks, generalists play a heretofore underappreciated role.

CHAPTER 1

SYNCHRONY IN SMALL MAMMAL COMMUNITY DYNAMICS ACROSS A FORESTED LANDSCAPE[1]

Abstract

Long-term studies at local scales indicate that fluctuations in abundance among trophically similar species are often temporally synchronized. Complementary studies on synchrony across larger spatial extents are less common, as are studies that investigate the subsequent impacts on community dynamics across the landscape. We investigate the impact of species population fluctuations on concordance in community dynamics for the small mammal fauna of the White Mountain National Forest, USA. Hierarchical open population models, which account for imperfect detection, were used to model abundance of the most common species at 108 sites over a three year period. Most species displayed individualistic responses of abundance to forest type and physiographic characteristics. However, among species, we found marked synchrony in population fluctuations across years, regardless of landscape affinities or trophic level. Across the region, this population synchrony led to high within-year concordance of community composition and aggregate properties (e.g., richness and diversity) independent of forest type and low among-year similarity in communities, even for years with similar species richness. Results suggest that extrinsic factors primarily drive abundance fluctuations and subsequently community dynamics, although local community assembly may be modified by species dispersal abilities and biotic interactions. Concordant community dynamics across space and over time may impact the stability of regional food webs and ecosystem functions.

[1]R. B. Stephens, D. J. Hocking, M. Yamasaki, and R. J. Rowe. 2017. Ecography 40: 1198–1209.

Introduction

Across systems and taxa, long-term studies at local sites indicate that interannual abundance dynamics among trophically similar species tend to covary positively and that changes in abundance among species frequently are synchronized over time (Houlahan et al. 2007). Complementary studies examining synchrony in abundance among species across a landscape are less common, and when considered, emphasis generally is on exploitative or coupled interactions such as predator-prey dynamics (Moran 1953, Ims and Andreassen 2000, Fox et al. 2013) or host-parasite relationships (Grenfell et al. 2001, Cattadori et al. 2005). Yet, most systems are composed of multiple interacting species within a guild or taxonomic unit and the degree of synchrony in their abundance fluctuations will influence community dynamics, and stability in those dynamics, over time and space.

Concordance describes the degree to which communities, drawn from the regional species pool, covary positively over time and space. High community concordance across a landscape may be driven by parallel responses of species to extrinsic factors of resource quality or availability, climate perturbations, or wide-ranging predators (Liebhold et al. 2004). In such cases, the degree to which life history traits or functional traits are similar among species contributes substantially to community dynamics (Loreau and de Mazancourt 2008, Stange et al. 2011). For instance, communities composed of species in different feeding guilds or trophic levels will be more robust to temporal changes of resources than communities of species consuming only one resource type. Likewise, species-specific phenologies or overwintering strategies will differentially impact the ability of species to respond to predatory or environmental perturbations. Thus, across-site comparisons of species abundance dynamics and their aggregate community impact provides a powerful framework in which to evaluate the

mechanisms structuring community dynamics (Stange et al. 2011, Michel et al. 2015). At the regional scale, this framework can also identify the role of habitat heterogeneity in shaping variability in community composition and aggregate properties of total abundance, richness, diversity, and evenness. Specifically, concordance across a landscape may be dampened by habitat heterogeneity which mediates competition among species and facilitates temporal stability of communities by providing greater refugia (Brown 2003). Understanding community concordance and the effect of habitat heterogeneity at the landscape scale has important implications for the structure and stability of food webs (Vasseur and Fox 2007, Gouhier et al. 2010) and for ecosystem function (Frost et al. 1995, Kent et al. 2007).

Small mammals (rodents and shrews < 250 g) are an excellent group for the study of community dynamics. They are diverse and are composed of members that vary considerably in their natural histories, often including a high degree of habitat and diet specificity (Reed et al. 2006, Stevens and Tello 2009, Stephens and Anderson 2014). Small mammals are also non-volant and are both short-lived and highly fecund, often producing multiple litters in one year (Egoscue et al. 1970). Subsequently, their populations are often more closely tied to local changes than those of more vagile animals, and their populations respond quickly to changes in climate and resource availability (Madsen and Shine 1999). These traits render small mammals especially well suited to the study of community concordance across large spatial scales such as a region. Moreover, because ecosystem functions provided by small mammals are largely dependent on species composition and numerical abundance, understanding dynamics at the regional scale may inform conservation and management efforts. In particular, small mammals are important vectors of zoonotic diseases (e.g., Lyme disease and Hantavirus; Ostfeld 1997, Yates et al. 2002) and can have profound effects on plant communities by directly consuming

vegetation or insect pests and by dispersing seeds and mycorrhizal fungal spores (Maser et al. 1978, Jensen and Nielsen 1986, Andersen and Folk 1993).

Here we use small mammals in the White Mountain National Forest (WMNF) to investigate the impact of fluctuations of individual species on community concordance across a heterogeneous landscape. By simultaneously investigating species responses, community composition, and aggregate properties we can enhance understanding of the causes and consequences of variability and stability of communities across ecological scales (Micheli et al. 1999, Rowe et al. 2011, Supp and Ernest 2014). The WMNF small mammal assemblage is diverse, composed of both shrews (primarily insectivorous) and rodents (largely granivorous, fungivorous, or herbivorous). We modeled abundance of individual species over a 2,100 km^2 expanse as a function of landscape variables and year while accounting for imperfect detection. Detection-corrected abundances of species were then compiled to examine spatial and temporal variability of communities over a three year period and across three dominant forest types. Our specific objectives were to 1) evaluate synchrony in abundance within and among multiple species relative to species traits and forest type, 2) determine the degree to which interannual dynamics in species abundance affect community composition and aggregate properties over space and time, and 3) determine the relative role of forest type and physiographic characteristics in structuring patterns of community similarity within and among years.

Methods

Study area

The White Mountain National Forest (WMNF) encompasses just over 3,000 km^2 in north-central New Hampshire and western Maine, USA. The region is mountainous with elevations ranging from 115 to 1,917 m. The climate is humid continental, characterized by

warm summers and cold winters with a steep climatic gradient from valley bottoms to mountain tops. Precipitation occurs evenly throughout the year and increases with elevation (Dingman 1981). During the late 1800s and early 1900s much of the low- and mid-elevation forests were cleared, followed by widespread fires fueled by residual slash (Belcher 1980). Today, approximately 97% of the WMNF is forested and, as a result of regeneration, the majority of stands are between 90 to 130 years old. Current localized disturbances include timber harvest, natural blow down, fungal pathogens, and ice damage. Low elevation mature forests are dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), eastern hemlock (*Tsuga canadensis*), and red spruce (*Picea rubens*), whereas early- and mid- successional forests are composed of paper birch (*B. papyrifera*), red maple (*A. rubrum*), poplar (*Populus* spp.), and white pine (*Pinus strobus*) (Leak 1991). Balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and red spruce dominate higher elevations (800 m to 1450 m) beyond which the forest grades into alpine tundra (Leak and Graber 1974, Reiners and Lang 1979).

Small mammal trapping

During the summers of 1995, 1996, and 1997, the United States Forest Service (USFS) used a stratified sampling approach to survey small mammals at 108 sites (36 each year; a given site was only sampled once during the three years) across a 2,100 km^2 expanse (Fig. 1.1). Elevation of sites ranged from 184 to 1092 m (mean 616 m) and cover types included hardwood (n = 39), mixed (n = 40), and softwood (n = 29) forests. Each site was sampled for 8 days in June and again in late July or August centered on the new moon phase (Prugh and Golden 2014). All sampling was removal sampling, and half of the sites (n = 54) were sampled using snap trap

grids and the other half using pitfall trap arrays. A given snap trap grid was paired with a pitfall trap array, with sites averaging 90 m apart (Fig. 1.1). We accounted for this paired arrangement and difference in trap type by using "location" as a random effect in our abundance modeling (see "Abundance modeling"). Snap trap grids consisted of a 5 by 5 station arrangement with 10 m spacing among stations (Fig. 1.1). Each station had three small Victor snap traps and one Museum Special for a total of 100 traps per grid. Traps were baited with a mixture of peanut butter and rolled oats and placed within 1.5 m of the station. Pitfall trap arrays consisted of 10 pitfall traps (2.8 L) arranged along three drift fence wings (made from aluminum flashing) forming a Y-shape with a pitfall trap at the mid-point and one pitfall at each end (Fig 1). An additional, isolated pitfall trap was placed at the centroid of each array. All traps were checked once daily for a total of 160 pitfall trap nights and 1,600 snap trap nights for a given location. Collected animals were bagged, labeled, and frozen for later identification. Forest Service staff performed all sampling operations and procedures adhered to guidelines outlined by the American Society of Mammalogists (Sikes et al. 2011).

Landscape variables

At each site we measured landscape variables likely to impact small mammal abundance. Within a 100 m buffer around each site, we used a GIS (ArcGIS v10.1; ESRI, Inc., Redlands, California, USA) to calculate physiographic characteristics (elevation and percent wetlands) and forest characteristics (percent forest cover type and age). Elevation was extracted from a digital elevation model (10 m resolution) obtained from the National Elevation Dataset (Gesch et al. 2002). We determined percent cover of wetlands or streams using the National Hydrologic Layer (Simley and Carswell 2009) with intermittent streams buffered by 2.5 m and perennial streams by 5

m. Wetlands and buffered streams were then merged into one layer and their area within each site buffer calculated. Forest cover type was derived from the 2001 New Hampshire Land Cover Data (NHLCD; http://www.granit.unh.edu/) and 2004 Maine Land Cover Data (MELCD; http://www.maine.gov/megis/catalog/; Smith et al. 2006). Using the majority rule in GIS, we resampled MELCD (5 m resolution) to match NHLCD (30 m resolution). Both data sets were reclassified into deciduous forest (hardwood), coniferous forest (softwood), mixed forest (mixture of deciduous and coniferous), and other. The proportion of hardwood, softwood, and mixed forest cover classes were assessed within each site buffer in FRAGTATS v4.2 (McGarigal et al. 2002). Forest age was calculated as the difference between the year a site was trapped and the average age of forest stands within a 100 m buffer, weighted by their relative area. Stand origin date was obtained from the WMNF forest stand layer (USFS, http://www.fs.usda.gov/main/whitemountain/landmanagement/gis) and represents the date a forest stand regenerated from a major disturbance (e.g., fire, hurricane, clear cutting) as estimated from a combination of early legal records, timber harvest sales, and tree cores. The accuracy of recent stand origin dates (< 35 years) were verified by overlaying orthophotos (1992) and digitized sale records provided by the USFS. Stands with no history of major disturbance (< 7% of buffers by area) were assigned the year 1600, approximating the age of old-growth forests in the region (Leak 1974).

Abundance modeling

We used count data from small mammal trapping to model abundance for the 15 most common species (nine rodents and six shrews from a 22 species assemblage; Table 1.1). A given site was trapped during one of the three years of sampling and we used these data to model

abundance for all three years. Thus, detection-corrected abundance estimates were generated at each site for each species in 1995, 1996, and 1997. We validated our technique using an independent data set (see "Model validation").

Using a hierarchical open population model within a Bayesian framework, we derived estimates of species abundance (λ), population change between sampling periods (γ), and probability of detection (*p*) from daily site captures from both June and late July/August sampling periods (Dail and Madsen 2011). Abundance in the first sampling period (June) was modeled as a function of covariates following a Poisson distribution with a log link,

$$N_{i,k=1} \sim Poisson(\lambda_{i,k=1})$$

$$log(\lambda_{i,k=1}) = \beta_{1[l]} + \mathrm{B}_1 X_{1[i]}$$

where $N_{i,1}$ is the abundance in the first sampling period $k = 1$ at site i, $\lambda_{i,k=1}$ is the mean expected abundance as a function of parameters $X_{1[i]}$ including trap type, year, elevation, stand age, stream and wetland area, percent hardwood, and percent mixed forest type, which vary by site i. Expected abundance was also adjusted by an intercept, $\beta_{1[l]}$, which varied randomly by location l (i.e., paired snap trap grids and pitfall arrays). The Dail-Madsen model is a generalization of the *N*-mixture model for repeated counts (Royle 2004), but allows for open populations (i.e., emigration and immigration) between sampling locations and intervals while simultaneously accounting for imperfect detection. The open period (time between sampling) was modeled using an auto-regressive function,

$$\log(\gamma_{i,k=2}) = \alpha_l + \delta[N_{i,1} - \sum_{j=1}^{J} y_{i,j,k=1}]$$

where $\gamma_{i,k=2}$ is the mean expected abundance in the second survey period (late July/August) over all sample nights J, α_l is an intercept that varies randomly by location, and δ is the change in

abundance from the end of the first survey to the start of the second survey. Because individuals were permanently removed during the first period, δ is multiplied by the abundance at the end of the first period ($N_{i,1}$ less the number of individuals removed, $\sum_{j=1}^{J} y_{i,j,k=1}$, during sampling). The abundance in the second survey period at site *i* is again assumed to follow a Poisson distribution:

$$N_{i,k=2} \sim Poisson(\gamma_{i,k=2})$$

We modeled change in abundance rather than separating apparent survival and recruitment, as described by Dail and Madsen (2011), because we lacked long time series with multiple open periods needed to distinguish the additional parameters.

Our modeling technique also explicitly accounted for imperfect detection. In the detection model, counts followed a multinomial distribution because individuals were removed from the population during sampling. The multinomial had eight categories, one for each survey night during the closed (i.e., sampling) period. Because the number of animals in the population decreased by the number of captures the previous night, probability of capture was adjusted accordingly,

$$y_{i,j,k} \sim Multin(N_{i,k}, p_{i,j=1:8,k})$$

where $y_{i,j,k}$ is the observed number of captures at site *i* on sample night *j*, during survey period *k* and $p_{i,j,k}$ is the associated probability of detection. The probability of capturing an individual may be affected by extrinsic parameters including environmental conditions (precipitation, minimum daily temperature, and minimum daily temperature^2) or trapping technique (snap trap and pitfall trap) and was therefore adjusted following a regression sub-model with a logit link,

$$logit(p_{i,j,k}) = \beta_{2[l]} + \mathrm{B}_2 X_{2[i,j,k]}$$

where $\beta_{2[l]}$ is an intercept that varies randomly by location *l*, B_2 is the vector of coefficients to be estimated, and $X_{2[i,j,k]}$ is the independent data matrix of parameters that vary by site, sample

night, and survey period. Trap type was included in both the detection and abundance portion of the model because it can affect the probability of catching an animal (detection) and the abundance of a species (i.e., snap trap grids and the pitfall arrays may sample different size areas and hence different population sizes). At the site level, we used PRISM climate data (PRISM Climate Group, http://www.prismclimate.org) at 4 km resolution in GIS to extract daily minimum temperature and precipitation that occurred while traps were open. We considered trap type as a binary covariate (0 = pitfall, 1 = snap trap).

The open population model was implemented in JAGS (Plummer 2003) via R 3.1.2 software (R Development Core Team 2014) using the package rjags (Plummer 2013). JAGS uses Markov Chain Monte Carlo (MCMC) methods, with a Gibbs sampler, to generate posterior distributions for model parameters. We ran three parallel chains of 100,000 iterations each, discarded the first 50,000 to avoid effects due to random starting values and thinned by 25. This left 6,000 iterations (2,000 per chain) to construct the posterior distribution. We chose non-informative priors to ensure that our inference was driven by the data. Specifically, we used a normal distribution with a mean of 0 and standard deviation of 10 (formulated as precision in JAGS; Plummer 2003) for all abundance covariate coefficients and uniform priors of -3 to 3 for all detection coefficients. For hyperpriors (standard deviation) of the random effects, we used uniform priors of 0 to 5 for population change and 0 to 10 for location effects on abundance. All continuous variables were z-standardized prior to analysis (i.e., subtracting the mean and dividing by the standard deviation). Model fit for each species was assessed using posterior predictive checks by visually comparing observed count data to posterior predicted count data generated from the model and ensuring that the Bayesian *p*-value of chi square test was near 0.5 (between 0.25 and 0.75; Kéry 2010). The effect of a given variable on a species' abundance was

interpreted as significant if zero was not included within 95% credible intervals. Code for implementing the model is available at: https://github.com/djhocking/Small_Mammal_Synchrony.

Model validation

Because our abundance and community analyses took advantage of model data both from years that were trapped and those that were not trapped, we used an independent data set from Bartlett Experimental Forest (BEF), central WMNF, to validate model predictability. These small mammal capture data came from four pitfall trap arrays (same setup as the regional sampling but without paired snap trap grids) in hardwood forest sites. Sites were surveyed in the same three-year period (each site surveyed 1995, 1996, and 1997) during which the WMNF dataset was collected, but were not included in the regional assessment.

To assess predictability, we ran our model for each species where one year of count data from the BEF sites, randomly selected for each site, was used to predict abundance for the other two years (predictions from training data). We then reran the model with all three years of BEF count data and estimated the abundance at each site and year to form a validation dataset. Both series of models used landscape variables, detection variables, and the three years of WMNF small mammal count data to derive abundance. For the six most common species, we assessed the models' ability to predict a species' abundance by using a Pearson's correlation between predicted abundance (using the training data) and expected abundance (from the model which included all validation data). Additionally, we assessed the effect of using predicted species abundance on community composition (see Community validation section).

Community properties and similarity

Using detection-corrected abundance data for the 15 most common species in the WMNF dataset, we quantified the following community properties of each site: total abundance (number of individuals across all species), richness (S = total number of species), diversity (Shannon Wiener index; $H' = -\Sigma\, p_i \ln[p_i]$, where p_i is proportional contribution of the ith species), and Pielou's evenness index ($J = H'/\log[S]$). We separately compared abundance, richness, diversity, and evenness across years within a forest type using a Friedman test (non-parametric repeated measures) and pairwise Wilcox tests to determine which years were different. We used a Kruskal-Wallis test and pairwise Wilcox tests for each metric within a year to determine if community properties differed by forest type. Non-parametric analyses were chosen due to deviations from normality within some groups.

We used a Bray Curtis dissimilarity matrix generated from detection-corrected abundance data for the 15 most common species to assess the effect of year and landscape variables on compositional similarity. To visualize trends in small mammal compositional similarity among years and forest types we used non-metric multidimensional scaling (NMDS), a robust unconstrained ordination method. Additionally, to facilitate comparison of our results to other studies, we complemented the NMDS with a similarity matrix. Matrix values were the mean pairwise Bray Curtis similarity (1 – Bray Curtis dissimilarity) of sites within and among forest types and years. We used PERMANOVA (multivariate repeated-measures ANOVA - function 'adonis' in R package Vegan; Oksanen et al. 2014) to quantify the role of year, forest type, and physiographic characteristics in structuring small mammal compositional similarity. We also tested for an interaction of year and forest type. We applied the repeated measures by using site as the nesting factor and assessed significance through comparisons with 999 randomized data

sets. In balanced sampling designs such as ours (i.e., same number of sites in each year), PERMANOVA can differentiate between location vs. dispersion effects, making it well suited for detecting differences in community similarity among sampling units (Anderson and Walsh 2013). When we detected a significant main effect of year, we conducted pairwise comparisons to determine which years had significantly different community composition. Significance levels were adjusted with Holm's correction for multiple comparisons (Holm 1979).

We assessed the effect of distance between sites on community similarity using Mantel tests. Within each forest type, in a given year, we assessed correlation between matrices of community similarity (Bray Curtis) and linear distance (km). If community similarity decreased with increasing linear distance we expected a significant *P*-value and the Mantel r statistic to have a negative slope. Mantel tests were performed using R package Vegan, and significance was assessed with a Monte-Carlo procedure with 999 permutations (Oksanen et al. 2014).

To determine if variation in community similarity differed among years or forest types within a year, we used the function 'betadisper' from R package Vegan (Oksanen et al. 2014). This analysis of dispersion compares the mean distance of group members to the group centroid, in this case year or habitat, and we interpreted results as a measure of relative concordance of communities across the landscape (lower multivariate dispersion = higher concordance). When significant, we used Tukey's post hoc tests between years or forest types within a year to determine pairwise differences.

Community validation

Our community level assessment of the WMNF sites used predicted abundance data and we tested the sensitivity of using these estimates in compositional similarity analyses by using

our BEF model validation dataset. We used an NMDS to compare community composition of each BEF site using abundances modeled from one year of observed count data (training set) to the community composition of the same BEF site in the same year using abundance data derived from a model with all three years of observed count data (validation set). Additionally, we tested if predicted abundance may have biased our community results within the WMNF dataset. We used a PERMANOVA (applied without the repeated measures), for each year, to assess if community similarity calculated from WMNF sites which were trapped in that year differed from sites which were not trapped that year (predicted abundance).

Results

Abundance of species

Over the three years, the USFS collected 8,780 individuals represented by 22 species from across 108 locations (Table 1.1). We modeled abundance as a function of detection and landscape variables for the 15 most common small mammal species (> 99.7% of total captures; Table 1.1, Fig. 1.2). Our model validation procedure indicated that our abundance modeling approach provides appropriate estimates for individual species (see "Model validation" below). Detection variables (trap type, precipitation, temperature, and temperature^2) were important in explaining heterogeneity of abundance for 10 species (Fig. 1.2). We described abundance variables in terms of trap type and landscape features including forest characteristics (age and forest type) or physiographic characteristics (elevation and percent wetlands). Trap type affected abundance for six species with a general trend of snap traps capturing more rodents and pitfall traps capturing more shrews. Of the landscape variables, forest characteristics were significant for six species and physiographic characteristics significant for four species (Fig. 1.2). The effect

of year (relative to 1995) on abundance was significant for seven species in 1996 and six species in 1997 (Fig. 1.2).

Six species comprised > 95% of the small mammal community (Fig. 1.3). Five of these dominant species showed great synchrony in response, displaying similar abundance changes across years with a dramatic decrease from 1995 to 1996 and then an increase from 1996 to 1997 (Fig. 1.3). The exception was the woodland jumping mouse (*Napaeozapus insignis*) which increased in abundance during 1996 and remained high during 1997 (Fig. 1.2, Fig. 1.3). Abundance trends were consistent across years irrespective of diet (i.e., insectivore, granivore, or herbivore; Fig. 1.3). Moreover, although the magnitude of a species response varied across forest types, the overall patterns did not (Fig. 1.3).

Model validation

Using our independent data from BEF we found agreement between abundance predicted during two of the years and abundance estimated from all three years of trap data. Both abundance estimates were highly positively correlated for five of the six species (Pearson's r = 0.83 to 0.99; Appendix B, Fig. B1), with the exception of the southern red-backed vole (*Myodes gapperi*; $r^2 = 0.23$), a species that was captured at very low abundances in BEF. Although our model tended to slightly under-predict higher abundances (Appendix B, Fig. B1), this result was minor and consistent across species and years, which likely is why predicted abundance had no observable influence on community metrics (see "Community validation"). Importantly, our BEF validation data come from one area and thus the observed pattern of under-predicted higher abundance likely indicates site-specific shrinkage toward the mean, such that other sites would

slightly over-predict. Together, these findings indicate that our open population model yielded robust estimates of abundance, even for years when trapping did not occur at a site.

Community properties and similarity

We quantified community properties in terms of abundance, richness, diversity, and evenness. These metrics differed across years, but were largely unaffected by forest type (Fig. 1.4). Mean site abundance was significantly different across all years with higher abundance in 1995 than 1997, and exceptionally low abundance in 1996. Abundance was the only metric that differed by habitat within a year and was higher in hardwood and mixed sites compared to softwood sites in 1996. This trend was likely due to the dominance of *N. insignis* in 1996 and its strong habitat affinity toward hardwood forests (Fig. 1.2, Fig. 1.3). Site richness was significantly affected by year, with less than half the number of species present in 1996 compared to either 1995 or 1997. Diversity was significantly different across all years and was highest in 1997 and considerably lower in 1996. Evenness was consistent across years with slight differences noted in mixed forest types between years.

At the regional scale, small mammal community composition was significantly affected by year and landscape characteristics (Table 1.2). However, year explained 50.9% of variation in community composition whereas forest and physiographic characteristics only explained a small portion of variation: forest type (4.0%), elevation (1.1%), percent stream/wetland (< 0.1%), and forest age (< 0.1%). The interaction of year and forest type was not significant, indicating that although communities changed across years, the relative effect of forest type stayed consistent (Table 1.2). Pairwise PERMANOVA comparisons between years indicated that each year had significantly different community composition: 1995 vs. 1996 ($F_{1,210}$ = 300.00, adj. P = 0.003),

1996 vs. 1997 ($F_{1,210}$ = 164.76, adj. P = 0.003), and 1995 vs. 1997 ($F_{1,210}$ = 69.99, adj. P = 0.003); however, year explained 56.1% of variance in community composition between 1995 and 1996 whereas it explained only 23.7% from 1995 to 1997 and 40.9% from 1996 to 1997. These trends were readily apparent in the NMDS ordination with strong clustering of communities by year along axis 1 and weak clustering by forest types within years along axis 2 (2 dimensions, stress = 0.119; Fig. 1.5a, 1.5b). Furthermore, based on Bray Curtis similarity, local communities were more similar across forest types within a year (0.58 – 0.70) than across years within a forest type (0.37 – 0.55; Fig. 1.5b, 1.5c). Within a year, there were no statistically significant correlations between linear distance of sites (avg. 26.8 km) and community similarity (Bray Curtis similarity) across a forest type (Table 1.3).

We detected significant differences in the degree of community similarity, or concordance, among years ($F_{2,321}$ = 15.85, P < 0.001). Tukey's post-hoc testing revealed that concordance was significantly higher in 1995 than in 1996 (P < 0.001) or 1997 (P = 0.003), and although there was not a significant difference between 1996 and 1997 (P = 0.059), there was a trend of 1996 having lower concordance than 1997. Differences in concordance among years were also visible in the NMDS plot with a greater spread among points in 1996 and 1997 compared to 1995 (Fig. 1.5a). Community concordance did not differ among forest types within a year: 1995 ($F_{2,105}$ = 0.222, P = 0.802), 1996 ($F_{2,105}$ = 2.007, P = 0.150), and 1997 ($F_{2,105}$ = 0.563, P = 0.583).

Community Validation

Similar to our species-level model validation, community trends were not biased by using model-predicted abundance data from years that were not trapped. Within a year, an NMDS

ordination of BEF communities using all three years of observed count data to estimate species abundances aligned with communities using just one year of data to estimate species abundance (Appendix B, Fig. B2). Additionally, both fell well within the yearly variation of the WMNF communities (Appendix B, Fig. B2). Among WMNF sites, there were no differences in composition when comparing communities with abundance from the year a site was trapped to communities with predicted abundance (years a site were not trapped) in 1995 ($F_{1,106} = 1.165$, $P = 0.312$), 1996 ($F_{2,106} = 1.54$, $P = 0.210$), or 1997 ($F_{1,106} = 0.98$, $P = 0.418$). This was also apparent in the NMDS ordination with all communities, within a year, clustering within the same space (Appendix B, Fig. B2), further supporting our use of predicted abundance data in our community analyses.

Discussion

For most species, we detected individualistic responses of abundance to forest or physiographic characteristics. However, among species, we found marked synchrony in population fluctuations across years, regardless of trophic level or landscape affinities. These parallel shifts in abundance led to largely concordant regional community dynamics within a year. At the community level, total abundance, diversity, and richness were similar among forest types within a year, but were significantly different within a forest type among years. Overall, year explained more than 50% of variation in community composition, whereas forest and physiographic characteristics collectively explained only 6% of variation. Studies at smaller spatial scales in the northeastern US have found similar trends with interannual abundance of species fluctuating synchronously across forest types, successional states, and elevation (DeGraaf et al. 1991, Brooks et al. 1998).

Growing evidence suggests that broad-scale community concordance may be common in many systems. For example, within Lepidoptera (Stange et al. 2011) and bacterioplankton (Crump and Hobbie 2005, Kent et al. 2007, Andersson et al. 2010) communities, abundance dynamics among taxa are consistently shown to be synchronized, even at the hemisphere-scale (Myers 1998, Crump et al. 2009). In small mammals, it is unclear how pervasive landscape concordance is among communities. Synchrony in population dynamics of small mammal species is common (Krebs and Myers 1974) and has been observed among species feeding at similar trophic levels (e.g., herbivorous arvicoline rodents; Krebs et al. 2002). Few studies have investigated landscape concordance among small mammal communities composed of species that vary in their natural histories (but see Korpimäki et al. 2005). Species-specific differences in ecological traits, in particular diet, may render idiosyncratic responses of species across a resource gradient or in response to punctuated availability of a resource type such as masting or insect outbreaks. Based on this assumption, one might expect asynchrony in community dynamics across a heterogeneous landscape. Yet, despite differences in forest type and physiographic characteristics and an assemblage composed of species with diverse natural histories, we demonstrate overwhelming similarity in community composition and structure across the region.

The WMNF small mammal assemblage is composed of species which are insectivores, granivores, fungivores, or herbivores (DeGraaf and Yamasaki 2001). Abundance dynamics of these species tracked similarly across forest types within a year, irrespective of diet, indicating that limiting food resources were likely not responsible for the observed synchrony. Rather, extrinsic factors likely caused the synchronous abundance dynamics we observed. Of the 15 most common species, only one showed a positive increase in abundance between 1995 and

1996. This species, the woodland jumping mouse, is the only obligate hibernator, suggesting a role in overwintering strategy in structuring its response. Merritt et al. (2001) also found population growth rates of woodland jumping mice to be inversely correlated with other small mammal species. This suggests extrinsic factors may have been acting on small mammal communities during the winter of 1995-1996 and that hibernation buffered woodland jumping mice from this perturbation. In studies of arvicoline rodents (voles and lemmings), multi-species synchrony in abundance is often driven by extrinsic factors of climate and predation (Hanski and Korpimaki 1995, Huitu et al. 2008). For overwintering populations, extreme climatic events during the winter or early spring may have disproportionately large adverse effects on population dynamics if resources are already limited (Hansen et al. 2013). Interestingly, lepidopteran dynamics are often synchronized across the WMNF (Stange et al. 2011), demonstrating that other groups may have similar responses to extrinsic factors such as climate.

Along with widespread synchronous declines of abundance from 1995 to 1996, we also observed a 50% loss in local species richness. In 1997 site richness was similar to 1995; however, community composition was markedly different and more variable, suggesting that dramatic synchronous declines permit the re-assembly of communities year to year and that dispersal plays a large role in structuring community composition (Thibault and Brown 2008). Comprehensive data on dispersal capacities for species in the region are lacking; nonetheless, body mass ranges from 2.9 ± 0.6 g (pygmy shrew [*Sorex hoyi*]) to 76.7 ± 10.0 g (eastern chipmunk [*Tamias striatus*]), suggesting that dispersal should vary considerably among species (Etienne and Olff 2004). Differences in dispersal contribute to colonization potential and the demographic success of species (Clobert et al. 2012). Furthermore, timing of colonization and its coincidence with availability of resources or the abundance of competitors also contribute to a

species ability to occupy a site (Davis et al. 2000, Shea and Chesson 2002). These processes may have led to the large variation in community composition among sites in 1997 compared to 1995, despite similar species richness. The greater similarity among communities during years of high abundance (i.e., 1995 compared to either 1996 or 1997 and a trend of 1997 being more concordant than 1996) may indicate that small mammals in the WMNF region operate under source-sink metacommunity dynamics. As local abundance increases in high quality patches, individuals disperse to lower quality patches (Matthysen 2005). At the species level, such density dependent dispersal may partially explain the relatively weak individualistic responses of species to physiographic characteristics compared to the year effect we observed. At the community level, high dispersal would homogenize the metacommunity (Mouquet and Loreau 2003), which may reflect the high concordance among communities we observed in 1995.

Overall, our observations raise the question of whether the WMNF landscape is indeed heterogeneous - at least as perceived by small mammals. Although three forest types are dominant (i.e., hardwood, softwood, and mixed), these forests have all regenerated from extensive clearing over a century ago, making them approximately even-aged. Thus, the region may superficially appear heterogeneous in forest type but may be homogenous with respect to structural complexity and resource availability, providing equal refuge among a suite of small mammal species that may otherwise discriminate (Lovejoy 1975, DeGraaf et al. 1991). Similar anthropogenic homogenization of forests in the western United States has ostensibly lowered local species richness (by selecting for generalist species) which subsequently reduced the complexity of the small mammal community (Kelt et al. 2013). In our study, forests averaged 119 (± 65) years old and only 6% of sites were < 50 years of age. Forest age was not an important predictor of abundance for the six most common species, but rarer species tended to

trend characteristically toward either older or younger forests (Fig. 1.2). In the WMNF, disturbances prior to intensive human land use consisted of fires and wind-throw, creating temporally intermittent and patchy forest openings of variable size embedded within a matrix of mature forest (Foster 1988, Cogbill 2000). Management strategies that retain mature forests and create a mosaic of forest clearings of early successional habitat across the landscape may emulate historical disturbances and promote greater biodiversity (North et al. 2009, North 2012). These management practices would maintain vertical complexity that accompany older forests and forest openings would increase habitat for uncommon early successional species such as the meadow vole (*Microtus pennsylvanicus*), ultimately increasing β-diversity across the landscape (Welsh and Healy 1993, Costello et al. 2000). Additionally, local studies investigating the effects of timber management on dominant small mammals in the WMNF indicate that the abundance of woodland jumping mice responds positively to structure associated with regenerating forest whereas abundance of deer mice (*Peromyscus maniculatus*) responds positively to characteristics associated with older forests (Lovejoy 1975, DeGraaf et al. 1991). Thus, the resultant heterogeneity of forest structure across the landscape may lead to greater partitioning among the more common forest dwelling species, ultimately reducing concordance of community dynamics (Brown 2003).

Given the importance of small mammals as critical prey and consumers in forested ecosystems (DeGraaf and Yamasaki 2001), community concordance may have implications for ecosystem structure and function. Particularly within the WMNF region, declines in species richness and aggregate abundance across the landscape could generate time-lagged fluctuations of predators specializing on small mammals such as the American marten (*Martes americana*) (Thompson and Colgan 1987). Moreover, the parallel loss of species feeding in multiple trophic

guilds indicates a cumulative reduction of ecosystem functions including consumption and dispersal of seeds, dispersal of mycorrhizal fungal spores, and regulation of arthropods. The lack of compensatory dynamics (*sensu* Houlahan et al. 2007) we document among the WMNF small mammal species may indicate that competition is less important than extrinsic factors in structuring community composition and dynamics in the region. However, differences in dispersal coupled with competition may be important for assembling local communities following broad scale synchronous declines. Future research will benefit from analyzing long-term dynamics of small mammal communities in the region to determine the role of competition, exogenous factors, and forest structure in generating the community structure and dynamics we observed.

Table 1.1. Captures of 22 small mammal species from 3 years of sampling in the White Mountains National Forest, New Hampshire and Maine. A total of 108 sites were surveyed, with 36 sites trapped each year. Order is based on the rank abundance of the three-year total. Abundance analyses were conducted for species in boldface type.

Species	Year			Total
	1995	1996	1997	
Sorex cinereus	1731	372	872	2975
Napaeozapus insignis	234	781	698	1713
Myodes gapperi	1192	60	240	1492
Blarina brevicauda	302	14	631	947
Peromyscus maniculatus	529	31	149	709
Peromyscus leucopus	287	15	185	487
Sorex fumeus	77	23	44	144
Sorex hoyi	37	10	39	86
Microtus pennsylvanicus	20	2	22	44
Sorex dispar	25	3	11	39
Zapus hudsonius	18	10	7	35
Synaptomys cooperi	19	1	6	26
Tamias striatus	10	5	8	23
Sorex palustris	9	5	6	20
Microtus chrotorrhinus	3	2	13	18
Glaucomys sabrinus	4	2		6
Glaucomys volans	3	2	1	6
Tamiasciurus hudsonicus	4			4
Condylura cristata		1	2	3
Microtus pinetorum		1		1
Parascalops breweri			1	1
Synaptomys borealis		1		1
Total	4504	1341	2935	8780

Table 1.2. PERMANOVA analysis showing the effect of year and physiographic characteristics on small mammal community composition across 108 sites. Distance among small mammal communities is based on a Bray Curtis dissimilarity matrix generated from detection-corrected abundances for the 15 most common species. We applied repeated measures by using site as the nesting factor.

Factor	Df	*F*-value	R^2	*P*
Year	2	188.865	0.5087	0.001
Forest type	2	14.738	0.0397	0.001
Elevation	1	8.260	0.0111	0.001
Stream/Wetland (%)	1	3.941	0.0053	0.001
Forest age	1	4.551	0.0061	0.001
Year x Forest type	4	1.639	0.0088	0.155
Residuals	312		0.4202	

Table 1.3. Results of Mantel tests comparing small mammal community similarity (Bray Curtis) and linear distance (km). Significance of Mantel tests was based on 999 permutations.

Forest type and year	Mantel r	*P*
Hardwood (1995)	0.0197	0.453
Hardwood (1996)	-0.1064	0.902
Hardwood (1997)	-0.0125	0.615
Mixed (1995)	-0.0535	0.796
Mixed (1996)	-0.2555	0.998
Mixed (1997)	-0.1930	0.986
Softwood (1995)	-0.2853	1.000
Softwood (1996)	-0.2614	0.999
Softwood (1997)	-0.2797	1.000

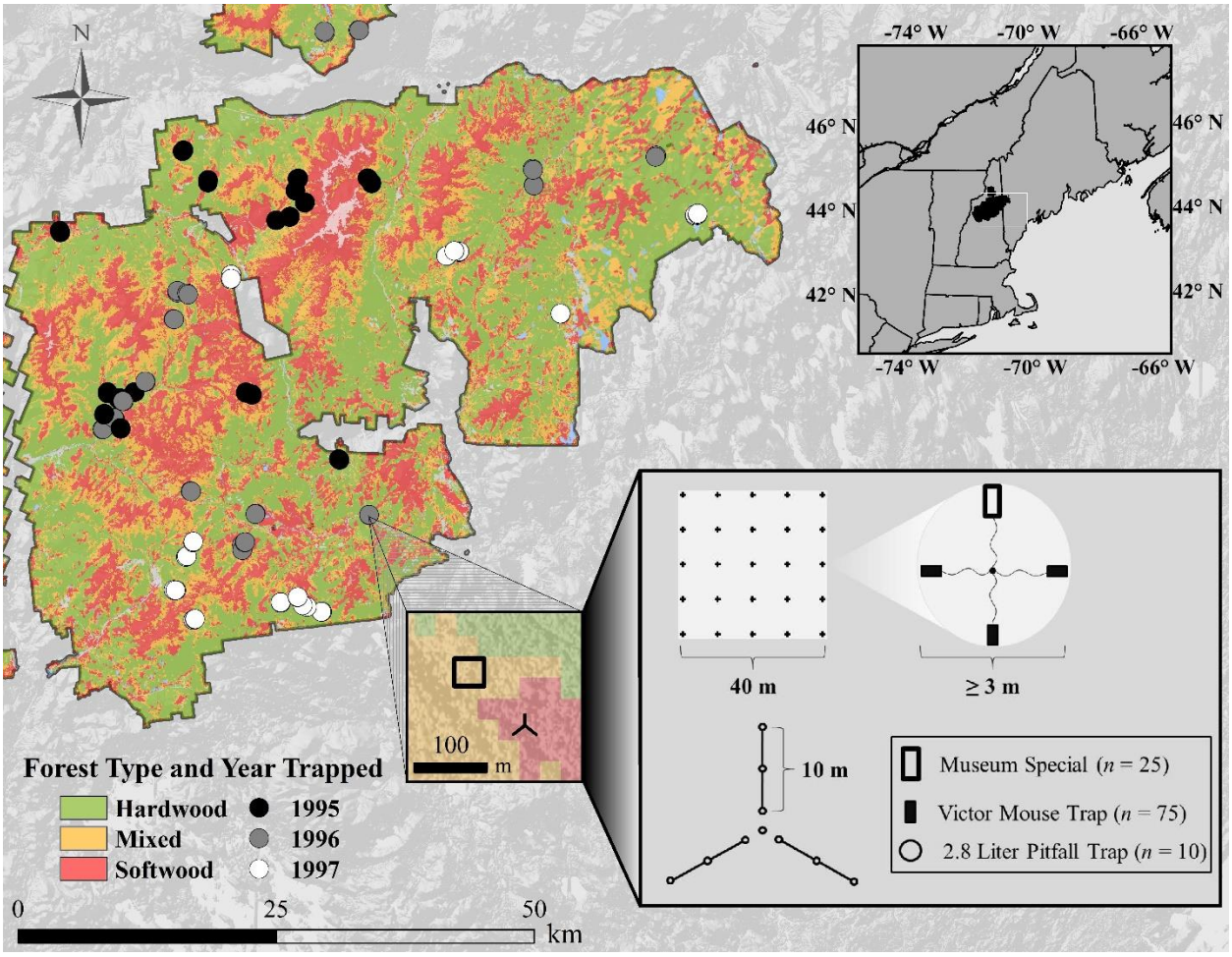


Figure 1.1. Distribution of sampling sites during the summers of 1995, 1996, and 1997 in the White Mountain National Forest, New Hampshire and Maine. In each year, 18 sites were trapped with snap trap grids and 18 with pitfall trap arrays. Snap trap grids consisted of 75 Victor snap traps and 25 Museum special snap traps. Pitfall arrays consisted of 10 -2.8 L pitfall traps arranged along three drift fences (see inset).

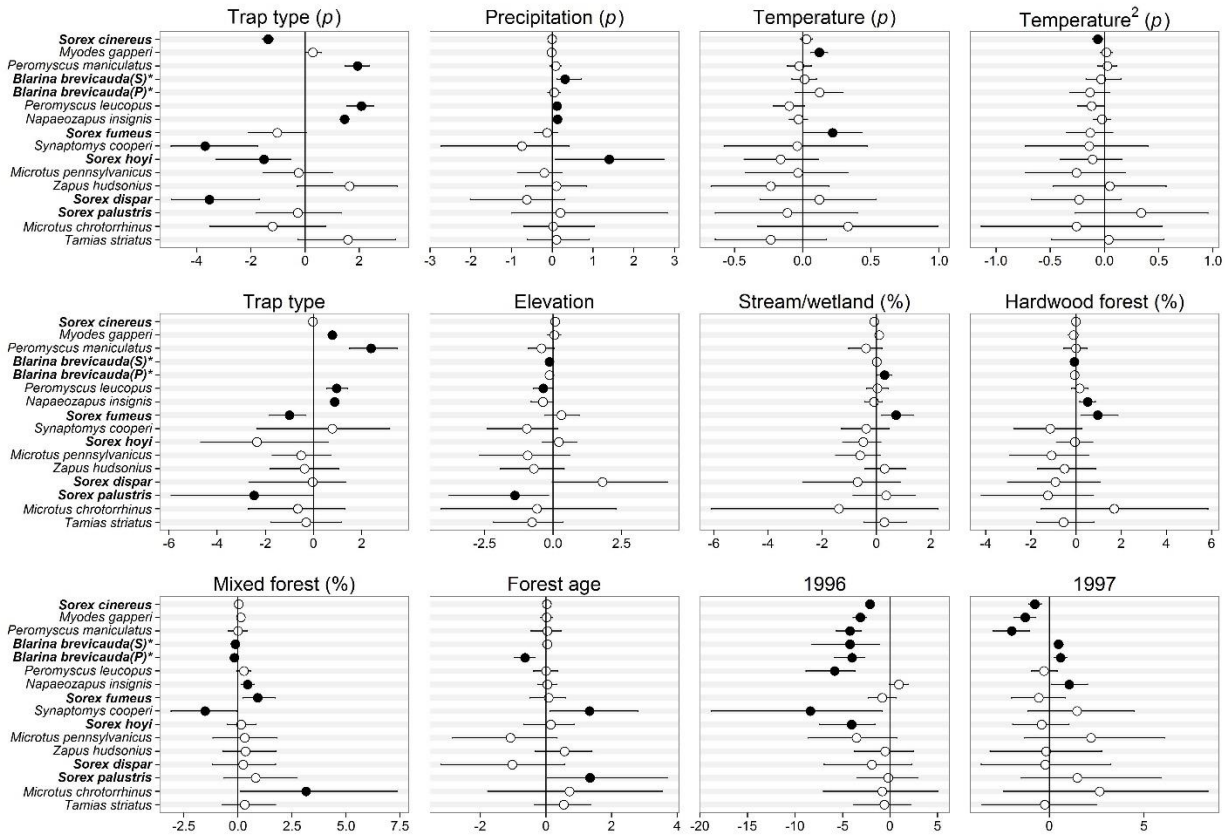


Figure 1.2. Results of an open population hierarchical model analyzed within a Bayesian framework for the 15 most abundant small mammal species. Species were modeled separately and are arranged from top to bottom in order of descending modeled abundance for 1995. Shrews are indicated in boldface type. Detection variables are indicated by (*p*). Circles indicate mean response in abundance or detection and error bars represent 95% credible confidence intervals. Closed circles indicate parameters for a species that do not contain zero within 95% credible intervals. The effect of hardwood and mixed forest is relative to softwood forest and the effect of 1996 and 1997 are relative to 1995. Positive values for trap type indicate an increased response to snap trap whereas negative values indicate an increased response to pitfall traps.

**Blarina brevicauda* were modeled separately for snap trap captures (S) and pitfall captures (P) due to non-convergence when abundance was modeled simultaneously.

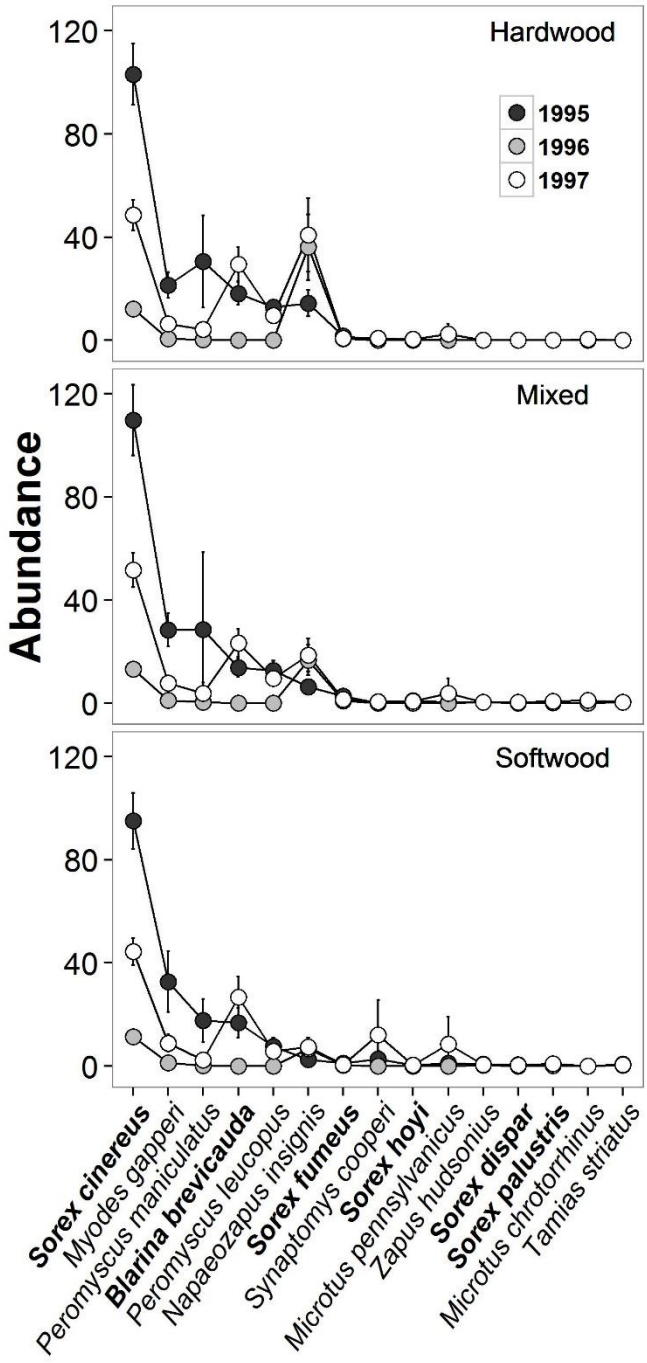


Figure 1.3. Mean site abundance as calculated from detection corrected abundance estimates for the 15 most common small mammal species at 108 sites in the White Mountain National Forest, New Hampshire and Maine. Plots are arranged by forest type: hardwood (top), mixed (middle), and softwood (bottom). Circles represent mean abundance for a given year and bars indicate 95% confidence intervals. Species are arranged from left to right in order of descending modeled abundance during 1995. Shrews are indicated in boldface type.

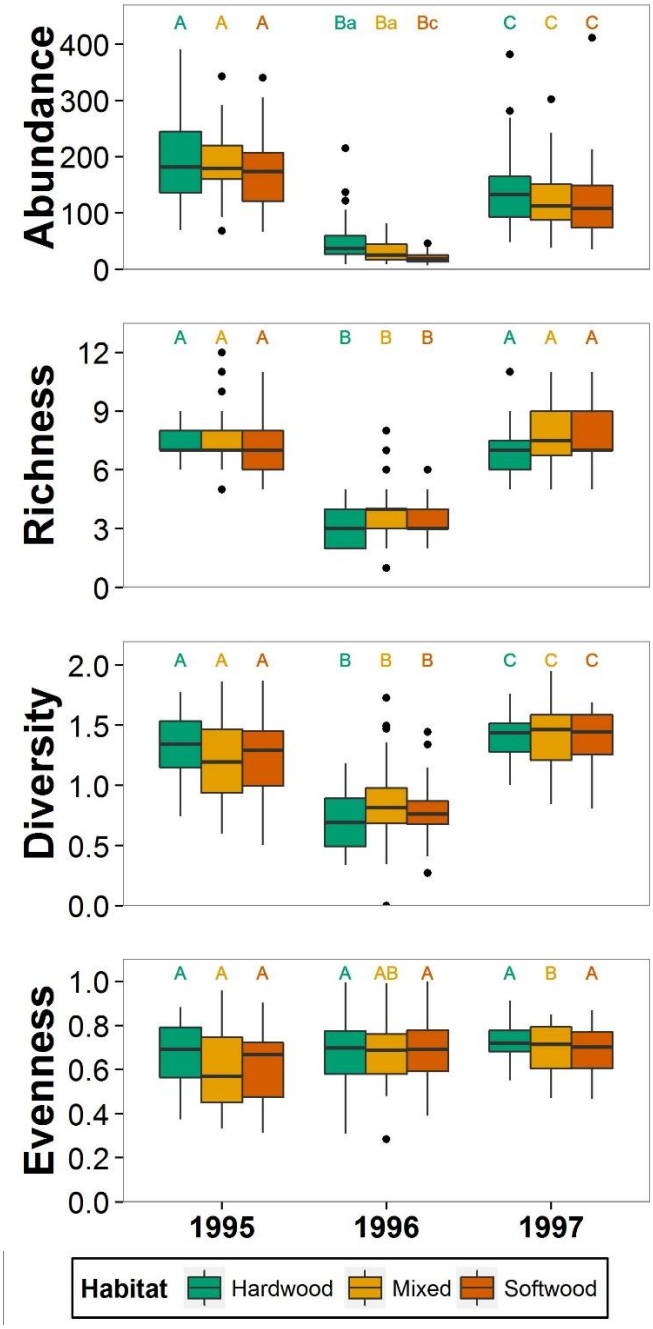


Figure 1.4. Box-and-whisker diagrams of four community metrics (abundance, richness, diversity, and evenness) for small mammals in hardwood, mixed, and softwood forests during each of the three survey years. Capital letters denote significant differences of a metric across years within a forest type based on Friedman tests and pairwise Wilcox tests, and lowercase letters denote significant differences between habitats within a year based on Kruskal-Wallis tests and pairwise Wilcox tests (only indicated for years with significant differences). Boxes with the same letters are not significantly different, whereas different letters indicate a significant difference. Corresponding test statistics for Friedman tests and Kruskal-Wallis tests can be found in Table B1 and B2, respectively of Appendix B.

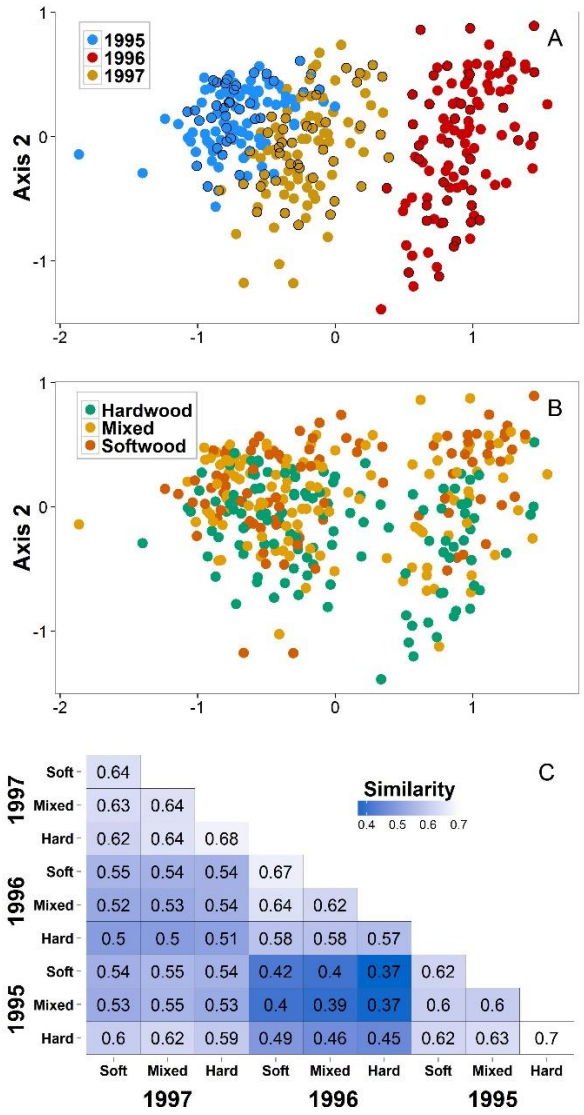


Figure 1.5. Similarity among small communities by forest type and year. Panels (A) and (B) are a two-dimensional nonmetric multidimensional scaling ordination of the 108 sampling sites over the 3 sampling years (324 total communities). Increased pairwise distance between sites (circles) indicates decreased similarity of community composition. Overlays represent small mammal community relationships with year (A) and forest type (B). The relative spread of sites within these categories can loosely be interpreted as the degree of community concordance. Outlined circles (A) represent communities composed of abundance data from sites which were trapped in that year, whereas circles without an outline represent communities composed of model predicted species abundance data (i.e., sites were not trapped in that year and species abundance data were predicted based on landscape variables, detection variables, count data from other sites trapped during that year, and count data from the year it was trapped). Panel (C) is a heat diagram of pairwise Bray Curtis similarity values (where 0 = completely dissimilar and 1 = identical) between forest types and years. Larger numbers and lighter colors indicate more similar communities. Abbreviations refer to forest type: Hard (hardwood, n = 39), Mixed (mixed, n = 40), and Soft (softwood, n = 29).

CHAPTER 2

DRIVERS OF TRUFFLE BIOMASS, COMMUNITY COMPOSITION, AND RICHNESS AMONG FOREST TYPES IN THE NORTHEASTERN US[2]

Abstract

Truffle-producing fungi (hypogeous sporocarps) are important mycorrhizal symbionts and provide a key food source for many animals, including small mammals. To better understand truffle diversity and associations in the northeastern US, we surveyed for truffles and analyzed spores in eastern chipmunk (*Tamias striatus*) scat across hardwood (angiosperm-dominated), softwood (gymnosperm-dominated), and mixed forest at Bartlett Experimental Forest, New Hampshire. Truffle biomass ranged from 3.8 kg/ha in hardwood forest to 31.4 kg/ha in softwood forest and was up to 35 times greater than mushroom (epigeous sporocarp) production in softwood forest. *Elaphomyces* species were the most common truffle taxa in both field surveys and chipmunk scat. Scat analysis indicated that truffle richness increased over the summer and accurately reflected fruiting time, providing greater resolution of richness than field surveys alone. Basal area of eastern hemlock (*Tsuga canadensis*) was the primary driver of *Elaphomyces* biomass and was the best explanatory variable of truffle community composition. We discuss implications of hemlock loss, due to the introduced hemlock wooly adelgid, on forest mycorrhizal communities and food webs.

[2]R. B. Stephens, T. J. Remick, M. J. Ducey, R. J. Rowe. 2017. Fungal Ecology 29:30-41.

Introduction

Mycorrhizal fungi form symbiotic associations with the roots of most vascular plant species, facilitating greater uptake of nitrogen, minerals, and water in exchange for carbohydrates (Smith and Read 1997). Inoculation of seedlings is especially important for the establishment and survival of many tree species (Terwilliger and Pastor 1999). In northern forests, the majority of tree species associate with either ectomycorrhizal or arbuscular mycorrhizal fungi. Trees in the families Betulaceae (birch), Fagaceae (beech and oak), and Pinaceae (pine, hemlock, fir, and spruce) associate with ectomycorrhizal fungi, while trees in the Aceraceae (maples) and Oleaceae (ash) associate with arbuscular fungi. Maintaining diverse mycorrhizal communities is vital for forest community composition and resilience to disturbance, with different mycorrhizal species enhancing plant growth and fitness seasonally and under differing environmental conditions (reviewed in Perry et al. 1989).

Many species of mycorrhizal fungi reproduce from sporocarps (fruit bodies) which may be above ground (epigeous) or below ground (hypogeous), hereafter respectively referred to as mushrooms and truffles. Quantifying abundance and community composition of mushrooms and truffles is important for assessing mycorrhizal responses to disturbance or successional state (Anderson et al. 2010, Tóth and Barta 2010). Sporocarps are also an essential component of the diets of many small mammal species (mice, voles, and chipmunks), with some obligate mycophagists (fungus eaters) depending almost exclusively on truffles throughout the year (Maser et al. 1978, 2008). Biomass and availability of truffles can be the best predictor of population density for mycophagists such as the northern flying squirrel (*Glaucomys sabrinus,* Gomez et al. 2005). In addition, a diverse truffle community is thought to be important because one fungal species alone cannot meet nutritional requirements due to variability in abundance

(Johnson 1994b), seasonality in fruiting (Vernes et al. 2015), and nutrient content (Dubay et al. 2008).

Across spatial scales, both abiotic and biotic factors act together to structure truffle abundance and diversity. At the local scale, abundance and diversity of truffles may be influenced by: soil nutrients (Danks et al. 2013), ground cover such as leaf litter depth or cover of woody debris (Amaranthus et al. 1994, Claridge et al. 2000); tree density (Luoma et al. 2004); and topographic features, such as aspect or distance from the riparian zone, which affect temperature or moisture regimes (Meyer and North 2005). At the forest stand scale, abundance and diversity of truffles is related to forest structure (Colgan et al. 1999) and community composition of tree species (Loeb et al. 2000). Seasonality in truffle fruiting is largely affected by temperature and moisture availability, especially in regions which experience punctuated precipitation events (e.g., Fogel 1976; Johnson 1994).

Assessing truffle abundance and diversity can be difficult due to seasonality in fruiting and patchy or clumped distributions. For this reason, it is important that sampling designs be both spatially and temporally replicated (Fogel 1976, Luoma et al. 1991, North et al. 1997). Additionally, mycophagy by small mammals can impact apparent abundance and diversity of truffles (e.g., Johnson 1994b; North et al. 1997). Small mammals can detect volatile compounds released by mature sporocarps buried in the soil (Donaldson and Stoddart 1994, Pyare and Longland 2001), and are able to target truffles that would otherwise be difficult to detect during field surveys (Johnson 1994b). After excavating truffles, small mammals consume the fleshy material along with microscopic spores which pass through the digestive system unharmed and are excreted in scat. Thus, small mammal scat may be an efficient way to document the presence and fruiting time of truffle taxa.

The abundance and diversity of sporocarpic fungi (mushrooms and truffles) has been poorly documented in the northeastern US, a region experiencing recent and increasing shifts in forest structure and composition (Orwig et al. 2002, Garnas et al. 2011). Understanding environmental associations and diversity of sporocarps can be used to help predict how these disturbances will alter the composition and structure of mycorrhizal communities and food web dynamics. Given the importance of sporocarps, particularly truffles, our goal was to identify biotic and abiotic factors associated with sporocarp biomass (or production) and diversity in mature, recently undisturbed northern forests. Our data come from spatially and temporally replicated field surveys among dominant forest types (hardwood, softwood, and mixed) and from collection of eastern chipmunk (*Tamias striatus*) scat. Eastern chipmunks are a widespread and abundant small mammal species in the Northeast and are known to consume fungi, including truffles, during the summer and fall season (Wrazen and Svendsen 1978, Teron and Hutchison 2013). Our specific objectives were to: (1) quantify the effect of local environmental factors on biomass of mushrooms (as a group) and the most abundant truffle species; (2) compare forest stand scale biomass (of truffles and mushrooms) and composition (of truffles) among forest types; and (3) determine if chipmunks consume sporocarps relative to their availability and if scat analysis can be used as an effective measure of fruiting time and availability of truffles.

Methods

Study area and sampling grids

Study sites were located at Bartlett Experimental Forest, White Mountain National Forest, New Hampshire (44° 3′ 7.2″ N, 71° 17′ 25.1″ W) at low elevations ranging from 250 to 450 m (Fig. 2.1A, 2.1D). The climate is humid continental and characterized by warm summers (mean July temperature, 19°C) and cold winters (mean January temperature, -9°C) with 127 cm

of precipitation distributed throughout the year (Richardson et al. 2007, King et al. 2011). Much of the study area was cleared for railroad fuel and limited agriculture during the late 1800s, and today mature forests are approximately 120 y old (Leak and Yamasaki 2010). Although Bartlett Experimental Forest continues to be harvested for timber, our site selection focused on mature forests in largely undisturbed stands. Forest stands fall into three main types based on their dominant tree species and include: hardwood dominated forest, softwood dominated forest, and mixed forest composed of both hardwood and softwood species. Hardwood and softwood refer to angiosperm and gymnosperm, respectively, consistent with use in the biological, ecological, and forest products literature and do not refer to wood properties (Mauseth 1988; Haygreen and Bowyer 1989). Dominant hardwood tree species include American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), sugar maple (*A. saccharum*), white ash (*Fraxinus americana*), and white birch (*B. papyrifera*). Dominant softwood tree species include eastern hemlock (*Tsuga canadensis*), red spruce (*Picea rubens*), and balsam fir (*Abies balsamea*). Eastern white pine (*Pinus strobus*) is occasionally present. Shrub cover ranges from depauperate to abundant with dominants including hobble bush (*Viburnum lantanoides*), striped maple (*Acer pensylvanicum*), witch hazel (*Hamamelis virginiana*), and tree saplings. Herbaceous cover is generally lacking with the exception of wet areas where sedges and ferns dominate. The soils are coarse-loamy well drained Spodosols developed from glacial till and are underlain by granite (Schaller et al. 2010). The ground is rocky with abundant small streams and ephemeral wetlands.

Sampling took place on 12 grids in mature hardwood (n = 4), mixed (n = 4), and softwood (n = 4) forest stands (Fig. 2.1D). Hardwood basal area averaged 91.0% (82.5 – 97.1%) in hardwood stands, 52.5% (45.4 – 62.9%) in mixed stands, and 25.5% (9.6 – 41.0%) in

softwood stands. Each grid consisted of an 8 x 8 station arrangement with 15 m spacing for a total of 64 stations encompassing an area of 11,025 m^2 (Fig. 2.1E). Average distance among grids was 1.23 km (range 0.28 - 2.61) overall, 1.42 km (range 0.84 – 2.12) among hardwood grids, 1.27 km (range 0.72 – 1.71) among mixed grids, and 1.45 km (0.38 – 2.54) among softwood grids.

Sporocarp and chipmunk sampling

In 2014 we assessed the abundance of fungal sporocarps at each of the 12 grids during four sampling periods spanning the growing season (in June, July, August, and September/early October). Green up at Bartlett Experimental Forest occurred from approximately May 23 through September 11 in 2014 (Richardson et al. 2007- https://phenocam.sr.unh.edu/webcam/). Within each grid, we sampled sporocarps at 16 of the 64 stations. Two stations were randomly selected from each of the eight grid columns to ensure even coverage (Fig. 2.1E). At each station, four plots (4-m^2) were established, one in each cardinal direction (2 m from the station) and randomly assigned to a different sampling month (Fig. 2.1E, 2.1F). Across a grid, 16 plots (4-m^2) were sampled in each month (one per station), for a total of 64 plots over the season (Fig. 2.1E). Clustered sampling at the station level allowed us to distinguish spatially aggregated fruiting patterns from temporal trends, and systematic rotation among grids allowed us to continuously sample each forest type over the summer season (Fig. 2.1C).

We delineated the plot boundary by scribing a 1.129 m radius (4-m^2 plots) from the plot center and used a short tined garden cultivator to remove leaf litter and excavate the organic soil layer to a depth of 10 cm or until mineral soil was reached (Luoma and Frenkel 1991). We thoroughly searched downed woody debris (DWD) in the later stages of decomposition when it occurred in a plot.

Mushrooms were also collected from the soil surface. All sporocarps were counted and placed in waxed paper bags labeled individually for each plot. In the lab, sporocarps were photographed, air dried for several days, thoroughly dried for 24 to 48 h at 60 °C in a drying oven, and weighed to the nearest 0.01 g (Luoma et al. 2004). Truffles were identified to species using published keys (Trappe et al. 2007, Beug et al. 2014) and confirmed by truffle experts (J. M. Trappe and M. Castellano). New species were formally described by Castellano and Stephens (2017), with the exception of one *Hysterangium* spp. nov. which awaits future description. Many mushrooms were not fully developed and because our focus was on truffles we did not identify these to any taxonomic level. Voucher specimens of representative truffle species were deposited in the Oregon State University Mycological Collection (OSC - Corvallis Oregon), US National Fungus Collections (BPI - Beltsville, Maryland), and the University of Florida Herbarium (FLAS - Gainesville, Florida).

As part of an on-going small mammal study, we collected eastern chipmunk scat 1 -7 d prior to sporocarp sampling in June, July, and August on each grid (Fig. 2.1B). The small mammal study protocol did not extend beyond August and trapping chipmunks prior to sampling sporocarps allowed us to assess consumption relative to availability prior to the disturbance of sporocarp sampling. Sherman live traps were baited with a bird seed mix and insulated with polyester batting. Traps were placed within 1.5 m of each station and checked twice daily over 4 d. Captured chipmunks were marked with a uniquely numbered ear tag and scat samples collected from the trap upon first capture of an individual during each survey period. Traps with captures were removed for washing and replaced with clean traps to ensure scat samples were from the individual in the trap. The trapping protocol was approved by the University of New Hampshire Animal Care and Use Committee (protocol 120708) and followed guidelines outlined by the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

Spore abundance in scat

Scat samples were frozen at -18 C° and prepared following methods similar to Vernes et al. (2001). Samples were freeze dried, cleaned of any debris, and ground to a powder using a glass micropestle in a 1.5 ml microcentrifuge tube. Approximately 20 mg of ground scat was weighed out to the nearest 0.1 mg into a 1.5 ml tube and 1 ml of 5% KOH added. The tube was shaken vigorously and allowed to stand for 5 min, after which the sample was rinsed through a 125 μm screen (Gerson Elite paint strainers; Middleboro, MA, USA) with 40 ml of distilled water. This solution was allowed to settle for 24 h in a 50 ml centrifuge tube and the resultant spore isolate was extracted using a pipette and mixed with 95% ethanol. This solution settled for an additional 1.5 h in a graduated microcentrifuge tube, after which we calculated the total volume of spore isolate using a micropipette. We spread 100 μl of spore isolate evenly on a glass slide onto a 22 x 22 mm area and added a drop of Visikol (chloral hydrate substitute- Phytosys LLC, New Brunswick, NJ, USA) and iodine. After drying, the slide was sealed with Flo-Texx mounting medium (Lerner Laboratories, Pittsburgh, PA, USA) and a cover slip.

Mycorrhizal taxa were identified to the lowest possible taxonomic unit using Castellano et al. (1989), published literature, and reference spores collected from sporocarps in the field. At 400x magnification, we counted the number of spores for each taxon within 25 non-overlapping fields of view distributed evenly across the slide (combined area of 4.15 mm^2; 1% of slide). Additionally, we scanned 121 mm^2 (25% of the slide) at 100x and counted spores of taxa that were not detected at 400x. For each magnification, we used standardized spore counts along with volume of spore isolate and scat weight to calculate total number of spores per taxon in 1 g of scat.

Spores in scat allowed us to quantify the types of mycorrhizal taxa present and their abundance. We qualitatively compared the fruiting time and availability of the most common truffle

species collected during field surveys to the frequency and abundance of spore loads in scat samples. Furthermore, we used the timing of spores in scat to infer fruiting time for rare taxa.

Environmental variables

For each grid we collected station level data on tree species (species specific basal area), ground cover (downed woody debris, leaf litter), and topography (distance to streams, slope). Using fixed area plots with a 5 m radius, we measured diameter at breast height (DBH) on trees ≥ 3 cm and calculated basal area (m^2/ha) for each tree species. Volume of DWD (m^3/ha) was calculated within a 2 m radius of each station and average leaf litter depth (cm) was calculated from two measurements taken 1 m from two sides of the station. All streams and wetlands within a 30 m buffer of the grids were mapped, georeferenced in ArcGIS v10.1 (ESRI, Inc., Redlands, California, USA), and the distance (m) from a station to the nearest stream or wetland calculated. If there were no streams within the 30 m buffer, we used the distance to the nearest stream as calculated from the National Hydrologic Layer (Simley and Carswell 2009). Using a digital elevation model (10 m resolution) from the National Elevation Dataset (Gesch et al. 2002), we calculated slope (degree) and extracted these values at the station level.

Environmental associations & biomass

For the six most common truffle species and mushrooms (as a group), we used linear mixed effects models to account for spatial variation and determine associations between local environmental variables and biomass (converted to kg/ha). We also used linear mixed effects models to estimate biomass among forest types. Mixed effects models were implemented with 'lme' using the 'nlme' package (Pinheiro et al. 2012) in R (R Development Core Team 2014). Due to great variation in

among plot biomass of *Elaphomyces* spp., these data were log transformed to improve normality and homoscedasticity.

As predictor variables, we considered basal area of dominant ectomycorrhizal tree species (balsam fir, American beech, eastern hemlock, red spruce, and yellow birch), volume of DWD, leaf litter depth, distance to stream, slope, and time (day of year [DOY] and day of year squared [DOY^2] to account for non-linear trends). Predictor variables were standardized to a mean of zero and unit variance, so that regression coefficients could be interpreted as relative effect strengths. We created separate models for each truffle species and mushrooms, but followed the same steps for model selection and validation. Grid, station, and forest type were included as random effects in the model. We included a random intercept for grid and station, which allowed us to capture heterogeneity at different spatial extents. More variation explained at the station level indicated clustered fruiting whereas more variation at the grid level suggested dispersed fruiting. We also included a multiple variance structure that allowed residual error to vary by forest type. Low levels of residual spread within a forest type indicated that most heterogeneity in biomass was explained by variables in the model, whereas large spread of residuals within a forest type indicated that other factors may be responsible for heterogeneity in biomass. The random intercept model and multiple variance models were sequentially compared to models without these components and the final random effects structure selected using Akaike's information criterion (AIC). We then selected fixed effects (environmental variables) by running a full model with all ten variables and the final random effects model structure. From this full model we used backward selection with stepAIC in the 'MASS' R package using unrestricted maximum likelihood (ML) to select the most parsimonious set of explanatory variables. Because restricted maximum likelihood (REML) is not defined in stepAIC, we then refitted the model using REML to obtain final model

coefficients (Zuur et al. 2009). Model fit was assessed by plotting residuals versus fitted values, and by evidence of homogeneity of variances and normality of both the residuals and random effects (Pinheiro and Bates 2000, Zuur et al. 2009).

We also used linear mixed effects models to estimate mean biomass (kg/ha) for total truffle standing-crop, total mushroom standing-crop, and the six most common truffle species among forest types. Differences between forest types were determined with Tukey's contrasts using 'glht' in the 'multcomp' R package (Hothorn et al. 2008). We fitted models using the same procedures outlined above for determining environmental associations, with the exception that the only fixed effect was forest type. We used log transformed biomass data for model selection and comparisons among forest types; however, we report means as kg/ha to allow comparisons with previous studies.

Truffle richness & community composition

We assessed patterns of truffle richness over time and among forest types using both field surveys and taxa detected in scat samples. For field surveys we calculated richness as the number of species detected on a grid within a sampling period (48 samples - 12 grids with 4 sampling periods). Truffle richness in scat samples was calculated by counting taxa within each sample (167 samples). Starting with a mixed effects modeling approach we assessed richness as a function of time (DOY) and forest type. The starting models included a random effect of station for field survey data and a random effect of station and individual chipmunk id for scat data (to account for correlation between scat samples from the same chipmunk), and both models included a multiple variance structure for forest type. However, these random effects and multiple variance structure by forest type did not improve model fit so we used multiple linear regression (function 'lm') in R for the final model.

We used field survey data to assess the effect of forest type and environmental variables on truffle community composition at the stand level. We used permutational multivariate analysis of variance (PERMANOVA- function 'adonis' in R package 'Vegan') on a Bray-Curtis dissimilarity matrix to assess similarity in fungal community composition across forest types. When significant, we conducted pairwise comparisons with PERMANOVA between forest types to determine which forest types were different. *P*-values were adjusted with Holm's correction to account for multiple comparisons (Holm 1979). Month was used as a nested factor and significance determined through comparisons with 999 randomized data sets. We used non-metric multidimensional scaling (NMDS), a robust unconstrained ordination method (function 'metaMDS' in R package 'Vegan'; Oksanen et al. 2014), on a Bray-Curtis dissimilarity matrix of sporocarp abundance to visualize patterns in truffle composition among forest types. Additionally, vectors of environmental variables were fitted to the NMDS ordination using function 'envfit' in R package 'Vegan' and significance assessed with 999 permutations to identify patterns between environmental variables and community composition. Environmental variables were averaged at the grid level and included basal area of the six most common tree species (eastern hemlock, red maple, American beech, red spruce, white ash, and yellow birch), leaf litter depth, volume DWD, and day of the year (Appendix C, Table C1). For both the PERMANOVA and NMDS we pooled sporocarp count data within a grid during each sampling period, totaling 47 samples (one hardwood site in September was excluded because no sporocarps were found).

Results

Sporocarps sampled from field surveys and as spores in scat

In a combined sampling area of 3,072 m^2 (768 - 4^2 m plots), we collected 6,334 truffles of 14 species representing seven genera and a total of 456 mushrooms (Table 2.1). Together, six species comprised > 99.8% of the total truffle abundance: *Elaphomyces verruculosus*, *E. macrosporus*, *E. americanus*, *Tuber shearii*, *E. bartlettii*, and *Hydnotrya cubispora*. Of these, the *Elaphomyces* spp. fruited all season long whereas mature *T. shearii* and *H. cubispora* were not detected until early August and late July, respectively (Fig. 2.2). Each of the eight remaining truffle species were only detected in a single sampling plot (Table 2.1). One non-*Elaphomyces* species did not have spores and could not be identified.

From 113 individual eastern chipmunks we collected 167 scat samples across hardwood (n = 53), mixed (n = 67), and softwood (n = 47) forest types. From scat, we detected a total of 28 fungal taxa including 20 truffle taxa represented by 13 genera and 8 mushroom taxa, most of which could only be identified to family or were not identified at all (Table 2.2). Truffle spores occurred in 166 chipmunk scats (99.4%), mushroom spores occurred in 121 scats (72.5%), and only one sample contained no fungal spores. The most commonly detected truffle taxa were *Glomus* (79.6%), *E. verruculosus* (58.1%), *E. macrosporus* (53.3%), *E. bartlettii* (34.1%), *Octaviania* (18.6%), *H. cubispora* (17.4%), and *E. americanus* (16.2%). All other truffle taxa occurred in less than 10% of samples (Table 2.2). The most commonly detected mushroom spores came from two unknown morphotypes (52.1% and 16.2%, respectively), Boletaceae (18.0%), and two taxa of Russulaceae (12.6% and 15.0%, respectively, Table 2.2). Spore loads varied greatly for both truffle and mushroom taxa and ranged from 101 spores/g at the lower end of our detectable limit to 916 million spores/g (Fig. 2.2; Appendix C, Fig. C1).

With the exception of *Tuber*, common truffle species found during surveys were consistently consumed by eastern chipmunks, and timing of spores in scat closely matched availability of mature

sporocarps (Fig. 2.2). Mature *Elaphomyces* sporocarps were available and consumed throughout the summer, and mature *H. cubispora* were first detected in late July which coincided closely with a spike in both incidence and spore loads in scat. Additionally, sporocarp abundance corresponded to frequency of spore occurrence among forest types for *E. verruculosus* (highest occurrence rates in mixed and softwood), *E. bartlettii* (highest in mixed forest), and *E. americanus* (similar among forest types; Table 2.1, Table 2.2). However, despite low biomass of *E. macrosporus* in hardwood forest, chipmunks consumed the highest amounts of this truffle species in hardwood forest. Similarly, *H. cubispora* was collected equally across forest types, but occurrence in scat samples increased from hardwood to softwood forest (Table 2.1, Table 2.2).

Nine truffle genera found in scat were only collected once ($n = 3$) or never collected ($n = 6$) during field surveys (Appendix C, Fig. C1). Of these, *Glomus* and *Gauteria* occurred in scat throughout the summer, whereas spores of *Endogone*, *Hydnobolites*, *Hysterangium*, *Octaviania*, and *Rhizopogon* were consumed in July and August and both *Leucogaster* and *Melanogaster* were not consumed until August (Appendix C, Fig. C1).

Environmental associations & biomass

We used linear mixed effects models to determine scale of fruiting pattern and environmental associations (ectomycorrhizal tree species, ground cover, topography, and time) for mushrooms and the six most abundant truffle species collected from field surveys. Of these, the four *Elaphomyces* species had a random intercept for grid (stand level scale) and station (local scale) in the optimal mixed effects model (Table 2.3). *Elaphomyces verruculosus* and *E. macrosporus* had more variation explained at the station level than the grid level, whereas *E. americanus* and *E. bartlettii* had similar errors at the grid and station level. All six truffle species and mushrooms included a multiple variance

structure with different residual error by forest type (Table 2.3). Differences in residual standard error among forest types for *E. americanus*, *H. cubispora*, and *T. shearii* were negligible. However, *E. verruculosus*, *E. macrosporus*, and mushrooms had higher residual error in mixed and softwood forest than in hardwood forest, and *E. bartlettii* had higher residual error in mixed than in hardwood or softwood forests.

Basal area of tree species was important for predicting biomass of four truffle species with *E. verruculosus*, *E. macrosporus*, and *E. bartlettii* positively associated with eastern hemlock and *E. americanus* and *E. bartlettii* negatively associated with red spruce (Table 2.3). Additionally, *E. bartlettii* was positively associated with yellow birch. Ground cover was important for predicting biomass of four species (Table 2.3). *Elaphomyces bartlettii* and *T. shearii* were positively associated with volume of DWD. *Elaphomyces verruculosus* and *T. shearii* were negatively associated with leaf litter whereas *E. macrosporus* was positively associated. Topography was not identified as important for explaining biomass for any of the species. Time was important for predicting the biomass of mushrooms and four truffles species (*Elaphomyces verruculosus*, *E. americanus*, *H. cubispora*, and *Tuber shearii*). Mushrooms and *Elaphomyces* spp. were positively associated with DOY and negatively associated with DOY^2 indicating a unimodal distribution with a midseason peak in biomass (Table 2.3). *Tuber shearii* was positively associated with DOY indicating a linear increase in biomass as the season progressed.

Linear mixed effects models were also used to compare biomass, among forest types, of total truffle, total mushroom, and the six most common truffle species. Overall, total truffle biomass was significantly lower in hardwood forest (3.8 ± 5.2 kg/ha) compared to mixed (26.6 ± 5.2 kg/ha) and softwood (31.4 ± 6.0 kg/ha) forest (Fig. 2.3). Mushroom biomass did not differ significantly across hardwood (0.5 ± 0.1 kg/ha), mixed (0.5 ± 0.3 kg/ha), or softwood (0.9 ± 0.3 kg/ha) forest types and

was 7.6 to 34.9 times lower than truffle biomass in hardwood and softwood forest, respectively (Fig. 2.3). Biomass of *E. verruculosus* was lowest in hardwood forest and highest in mixed and softwood forest. This dominant species contributed 69.4% of total biomass in hardwood forest, 84.4% in mixed forest, and 90.1% in softwood forest. Similar to *E. verruculosus*, biomass of *E. macrosporus* was lowest in hardwood forest and highest in softwood forest, whereas *E. bartlettii* was lowest in hardwood and softwood forest and highest in mixed forest. Biomass of *E. americanus*, *T. shearii*, and *H. cubispora* were not significantly different across forest types.

Truffle richness & community composition

Results of a multiple regression analysis indicated that truffle richness from field surveys (adj. $R^2 = 0.14$, $F_{3,44} = 3.61$, $P = 0.020$) was consistent over the fruiting season whereas richness in scat (adj. $R^2 = 0.21$, $F_{3,162} = 15.60$, $P < 0.001$) increased over the summer season (Fig. 2.4A, 2.4B; Table 2.4). Both field surveys and scat samples showed lower richness in hardwood than in mixed or softwood forest; however, the trend of higher richness in softwood than hardwood forest was not significant for chipmunk scat (Fig. 2.4A, 2.4B; Table 2.4). Lack of significant differences between these forest types likely had to do with limited chipmunk captures in softwood forest in June (Fig. 2.1B).

Based on a PERMANOVA evaluating the effect of forest type on truffle species composition, we found that forest type explained 31.7% of variation in truffle composition ($F_{2,44} = 10.19$, $P < 0.001$). Pairwise PERMANOVA comparisons between forest types showed composition to be significantly different between hardwood and mixed forest ($F_{1,29} = 9.37$, adj. $P = 0.003$) and hardwood and softwood forest ($F_{1,29} = 16.07$, adj. $P = 0.003$), but similar between mixed and softwood forest ($F_{1,30} = 2.10$, adj. $P = 0.114$). This was apparent in the NMDS ordination with strong clustering among mixed and softwood forest communities and separation

of hardwood forest communities along NMDS axis 1 (2 dimensions; stress = 0.087). Our *envfit* analysis revealed that eastern hemlock was the most highly correlated environmental variable with truffle community composition ($r^2 = 0.610$, $P < 0.001$). American beech ($r^2 = 0.482$, $P < 0.001$), leaf litter depth ($r^2 = 0.437$, $P < 0.001$), red spruce ($r^2 = 0.282$, $P = 0.003$), red maple ($r^2 = 0.200$, $P = 0.009$), and white ash ($r^2 = 0.189$, $P = 0.012$) were also significant (Fig. 2.4C; Appendix C, Table C1).

Discussion

The goal of this study was to better understand sporocarp production and diversity in the northeastern US. The majority of sporocarp production was in the form of truffles which reached up to 31.4 kg/ha in softwood forest and was 35 times higher than mushroom biomass. The hypogeous habit of truffles buffers them from drought or frost conditions that would otherwise prohibit production of mushrooms (Thiers 1984, Trappe 1988). The Northeast is characterized by warm summers and cold winters and fruiting below ground likely extends the fruiting season of truffles over that of mushrooms. This is particularly true of *Elaphomyces* spp. which were abundant throughout our sampling period and fruit well into the fall and winter (Castellano and Stephens 2017). Over 99% of the total truffle biomass was contributed by *Elaphomyces* spp., a genus that has both a relatively long maturation time and large sporocarp and fruiting cluster size compared to other genera (Hunt and Trappe 1987, North and Greenberg 1998). The overall abundance and yearlong availability of *Elaphomyces* sporocarps makes them an important food source for small mammals, despite being low in digestibility relative to seeds (Cork and Kenagy 1989a). Indeed, we found spores of *Elaphomyces* spp. were among the most commonly consumed truffle taxa by eastern chipmunks. Additionally, Vernes et al. (2004) found that northern flying squirrels (*Glaucomys sabrinus*) and red squirrels (*Tamiasciurus hudsonicus*) consumed *Elaphomyces* throughout the year in New Brunswick, Canada.

Vernes et al. (2004) postulated that these sporocarps may be extremely important for filling seasonal gaps in food availability such as when tree mast is not available. We found that most production of *Elaphomyces* spp. was associated with eastern hemlock, a tree species in decline due to an invasive insect pest. Loss of eastern hemlock and subsequent reduction in truffle production may have cascading effects on forest food web dynamics, notwithstanding reduced dispersal of spores to other ectomycorrhizal tree species.

Compatibility of scat and field surveys

All but one sample of eastern chipmunk scat contained spores from truffle taxa, suggesting that truffles are a common and important component of chipmunk diets throughout the summer season. Although fungal consumption in sciurids (squirrels, chipmunks, and their relatives) can vary among seasons as food resources change (e.g., seed abundance; Vernes et al. 2004) or with density, our chipmunk sampling took place during one season (summer) where food availability should have been relatively constant across forest types (i.e., most seeds are available in the fall). Additionally, the number of chipmunks was similar across forest types with an average of 8.8 individuals in hardwood grids, 11.8 in mixed grids, and 8.8 in softwood grids. Overall, chipmunks consumed more truffle taxa than were detected during field surveys. However, for most of the commonly consumed truffles, consumption reflected abundance from truffle field surveys. Additionally, for three of the most common *Elaphomyces* spp., consumption mirrored availability across forest types. Interestingly, although *Glomus* was detected in nearly 80% of scat samples it was never collected during field surveys. *Glomus* is an arbuscular mycorrhizal genus with some species fruiting as sporocarps and others as individual spores in the soil (Castellano et al. 1989). *Glomus* sporocarps tend to be very small, often measuring < 1 mm in diameter (Almeida and Schenck 1990). This small sporocarp size

may have limited their detection during field surveys and detection of individual spores in the soil would not be possible without wet-sieving and microscopy.

These results suggest that field surveys are biased toward the collection of common truffle species of larger size whereas mycophagous small mammal scat contains rare and small truffles that would otherwise be difficult to detect during field surveys. Other studies looking at mycophagous mammal scat have found similar results with mammals consuming more taxa than discovered during field surveys (e.g., Johnson 1994b; Carey et al. 2002). Highest spore loads in scat generally occur within 24 h of consumption and most spores are passed within 3 d (Cork and Kenagy 1989b, Danks 2012). Moreover, although eastern chipmunks can occasionally move long distances, their home range is generally less than 1 ha (Yerger 1953, Snyder 1982). Consequently, scat samples capture the presence of mature sporocarps near the time of fruiting and close to the area where they were consumed. However, dispersal of spores by chipmunks would preclude the use of scat to identify fine-grained patterns of spatial association between truffle species and environmental variables such as microtopography and tree species abundance in heterogeneous forests.

In our study, both field surveys and chipmunk scat showed similar patterns of truffle richness among forest types, but spore richness in scat increased over the summer whereas field surveys showed that richness was static. Thus mycophagous mammal scat may be better for detecting truffle richness patterns due to their ability to detect rare truffle taxa. Because field surveys can disturb soil, analysis of scat may be preferable in cases where destructive sampling is not possible, such as in protected areas. Nevertheless, a limitation to using spores in scat is that it can be difficult to identify spores past the genus level, especially if spore morphology of species is not known. Genetic analysis of scat may help to identify spores to the species level, but without voucher sporocarps for species it would not be possible to identify undescribed species which are often common in areas where truffle

surveys have not previously been carried out (e.g., Danks et al. 2013; Castellano and Stephens 2017). Consequently, combining these methods to assess truffle richness and diversity in a region is advantageous.

Temporal and spatial fruiting

Based on chipmunk scat analysis, richness of truffle taxa fruiting increased linearly from early June to mid-August. Although we do not have data for the fall season, number of truffle taxa in the scat of other sciurid species (red squirrel and northern flying squirrel) was higher in the summer than either the spring or fall season in New Brunswick, Canada (Vernes et al. 2004). The summer peak in fruiting phenology observed in our chipmunk scat may correspond with soil temperature or available photosynthate from host trees. These factors may also explain the midseason peak in biomass we observed for mushrooms and most truffle species.

Truffle fruiting is spatially variable and failure to account for this heterogeneity can lead to biased estimates of production (reviewed by Luoma and Frenkel 1991). Robust sporocarp sampling (e.g., spatially and temporally replicated plots) coupled with mixed effects models may offer an approach to understand spatial fruiting pattern, which is often species specific. In our mixed effects models, variance was partitioned into components at the local scale (station) or forest stand scale (grid) and residual (unexplained) error was allowed to differ across forest types. Greater variance at the local scale than forest stand scale was evident for the two most common species, *E. verruculosus* and *E. macrosporus*, and indicates they fruit in large clusters. Other species that generally fruited as single sporocarps or in small clusters had similar variability at the local and stand scale (*E. americanus* and *E. bartlettii*) or did not have these terms included in the best model (*H. cubispora* and *T. shearii*). The scale at which sporocarps are distributed has important implications for foraging effort of

mycophagous animals (Clarkson and Mills 1994, Gomez et al. 2005). Our data suggest that abundant species that fruit in large clusters (i.e., *E. verruculosus* and *E. macrosporus*) are commonly consumed by chipmunks and are likely easier to detect compared to species that fruit as singletons which may require more foraging effort (Table 2.2).

For all truffle taxa, the amount of unexplained variation differed among forest types. This variation was greatest for species associated with eastern hemlock. In hardwood forest stands, hemlock basal area explained most of the variation in biomass for the two most common species, *E. verruculosus* and *E. macrosporus*, despite hemlock trees occurring at low densities. Indeed, in hardwood forests, clusters of *E. verruculosus* and *E. macrosporus* sporocarps were exclusively collected around the base of lone hemlock trees, some of which were only 9 cm in diameter. Comparatively, in mixed and softwood forest where eastern hemlock was abundant, unexplained variance in biomass of *E. verruculosus* and *E. macrosporus* was high. We measured basal area of trees within a 5 m radius of the station; however, sporocarp fruiting peaks at 2 m from the base of trees (Fogel 1976, North and Greenberg 1998). This mismatch in scale may contribute to greater variance at the station level in mixed and softwood forest. Additionally, local scale heterogeneity in *Elaphomyces* sporocarp biomass is often driven by organic horizon depth and root density, with more biomass associated with deeper organic matter and higher root density (North and Greenberg 1998). Although we did not explicitly model sporocarp biomass as a function of organic layer depth, our soil profile sampling on grids suggests that organic soil is deeper and more variable in mixed (15.8 ± 7.1, range 3 to 32+ cm) and softwood forest (15.4 ± 6.2, range 4 to 31+ cm) compared to hardwood forest (7.1 ± 4.0, range 1 to 17 cm). This heterogeneity in soil organic matter depth may further explain local scale fruiting of these abundant species. Greater heterogeneity of species biomass in mixed and softwood forest stands may also be due to a higher richness of ectomycorrhizal host trees. These host trees could

support ectomycorrhizal taxa which compete for space or other resources. This may explain the negative associations of *E. americanus* and *E. bartlettii* with red spruce.

Drivers of truffle biomass and community composition

In regions where precipitation is seasonal, decaying downed wood is often the best predictor of truffle richness and biomass (Clarkson and Mills 1994, Amaranthus et al. 1994). These structures can hold more water than surrounding soil and may provide consistent moisture for sporocarp production. We found that only two species were positively associated with downed woody debris, *T. shearii* and *E. bartlettii*. *Tuber shearii* was only associated with ground cover variables whereas *E. bartlettii* was also associated with basal area of tree species and is likely not as restricted to logs as *T. shearii* (found nearly exclusively in decaying logs). This general lack of individual species and community association with decaying logs in the Northeast, where rain generally falls evenly throughout the year, may indicate that moisture is a not limiting factor for sporocarp production.

Although other ectomycorrhizal tree species including American beech and red spruce were common at Bartlett Experimental Forest, basal area of eastern hemlock was by far the best explanatory variable of biomass for the dominant *Elaphomyces* spp. and truffle community composition. This association with hemlock, which primarily occurred in mixed and softwood forest, lead to higher standing crop and similar truffle communities in mixed and softwood forest compared to hardwood forest. In the Pacific Northwest, stands dominated by western hemlock (*Tsuga heterophylla*) also have *Elaphomyces* spp. as a common associate and support high truffle standing crop compared to stands without western hemlock (e.g., North et al. 1997; North and Greenberg 1998). Deep soil organic matter accumulations under hemlocks may help promote sporocarp production of *Elaphomyces* spp. (North and Greenberg 1998, Campbell and Gower 2000).

Additionally, soils in hemlock dominated stands are more acidic and have a lower water content than maple dominated stands (Daubenmire 1930), and these conditions may also favor *Elaphomyces* species.

Because hyphae of *Elaphomyces* associate with a broad host group including both angiosperms and gymnosperms (Trappe 1979), sporocarp production associated with eastern hemlock, and subsequent dispersal of spores by small mammals, may be key for inoculating roots of other ectomycorrhizal tree species. Additionally, small isolated eastern hemlock trees are capable of facilitating sporocarp production, suggesting that even at low density eastern hemlock likely plays an important role in providing mycorrhizal inoculum at the stand level. Furthermore, isolated eastern hemlocks provide a food source for small mammals in hardwood dominated forests. In our study, chipmunks consistently consumed sporocarps of *E. macrosporus* in hardwood forest, despite very few eastern hemlocks in the forest stands.

Hemlock decline and ecosystem consequences

Eastern hemlock is a long-lived and common forest associate throughout New England. The distribution and abundance of this species is currently imperiled by the invasive hemlock wooly adelgid which has resulted in widespread mortality in southern New England (Orwig and Foster 1998). Presently, the adelgid is limited by cold winters but rising winter temperatures, as a result of climate change, are predicted to facilitate its movement into northern New England where its impact may be dramatic as hemlock is a dominant forest component (Paradis et al. 2008). Even live trees infested with the adelgid have a 67% decrease in root tip colonization by ectomycorrhizal fungi (Vendettuoli et al. 2015), and reduced colonization would decrease carbon allocation to fungi and result in lower truffle production. Such results would reduce available

inoculum for other ectomycorrhizal tree species and food for mycophagous small mammals which are the prey base for many avian and terrestrial predators (Portnoy and Dodge 1979, Thompson and Colgan 1987). Effects on food web dynamics may be particularly severe when other food items are limited such as years of low seed or mast availability (Vernes et al. 2004). Finally, loss of hemlock may reduce mycorrhizal diversity. For example, truffle production of the recently described *E. macrosporus* and *E. bartlettii* seem to be exclusively associated with eastern hemlock (Castellano and Stephens 2017).

Conclusions

Truffles are important components in forest ecosystems, yet with the exception of portions of eastern Australia and the northwestern US, their environmental associations and diversity are poorly known (Maser et al. 2008). We used field surveys and analysis of spores in chipmunk scat to investigate truffle production and diversity in the northeastern US, a region that has been little explored for truffle diversity. Field surveys and mycophagous mammal scat were complementary for describing the truffle flora of a region, with field surveys better able to determine species level identifications and drivers of truffle biomass whereas analysis of mycophagous small mammal scat was useful for elucidating truffle richness and seasonality in fruiting. We found that truffle production and community composition was largely driven by eastern hemlock and that loss of this tree species will likely change mycorrhizal communities and forest food web dynamics. In other regions where truffles are poorly known, coupling field surveys with scat analysis may be an efficient way to characterize species associations and diversity. Identifying drivers that shape truffle richness and diversity among regions will help promote a more synthetic understanding of the distribution and ecology of hypogeous fungi.

Table 2.1. Total number and frequency (percent of 4-m^2 plots with ≥ 1 sporocarp) of truffle and mushroom sporocarps across forest types from field surveys. Number of plots sampled was 256 in each forest type for a total of 768 plots across all forest types. Taxa are arranged from most abundant to least abundant and those with the same total number are arranged alphabetically by genus. Number and frequency were calculated separately for truffles and mushrooms.

Taxon	Forest Type						Total	
	Hardwood		Mixed		Softwood			
	Total	Freq.	Total	Freq.	Total	Freq.	Total	Freq.
Truffle								
Elaphomyces verruculosus	301	3.9	2117	28.5	2928	51.2	5346	27.9
Elaphomyces macrosporus	65	4.3	257	14.1	252	19.5	574	12.6
Elaphomyces americanus	69	14.1	91	13.7	88	13.7	248	13.8
Tuber shearii	7	2.0	11	0.8	50	2.7	68	1.8
Elaphomyces bartlettii	8	0.4	43	5.1	7	2.0	58	2.5
Hydnotrya cubispora	6	1.6	11	3.1	11	2.7	28	2.5
Elaphomyces remickii			2	0.4			2	0.1
Genea brachytcheca			2	0.4			2	0.1
Octaviania zelleri	2	0.4					2	0.1
Elaphomyces oreoides	1	0.4					1	0.1
Hydnotrya tulasnei	1	0.4					1	0.1
Hysterangium spp. nov.					1	0.4	1	0.1
Rhizopogon truncatus			1	0.4			1	0.1
Tuber cf. *anniae*					1	0.4	1	0.1
Unknown	1	0.4					1	0.1
All taxa	461	23.8	2535	46.1	3338	64.1	6334	44.7
Mushroom								
All taxa	154	25.8	143	20.3	159	26.2	456	24.1

Table 2.2. Percent of eastern chipmunk scat samples containing truffle and mushroom sporocarps across forest types. Taxa are arranged from most abundant to least abundant and those with the same total number are arranged alphabetically by genus.

Taxon	Forest type			
	Hardwood	Mixed	Softwood	Total
Truffle				
Glomus	73.6	85.1	78.7	79.6
Elaphomyces verruculosus	35.8	73.1	61.7	58.1
Elaphomyces macrosporus	62.3	44.8	55.3	53.3
Elaphomyces bartlettii	26.4	44.8	27.7	34.1
Octaviania	32.1	9.0	17.0	18.6
Hydnotrya cubispora	5.7	17.9	29.8	17.4
Elaphomyces americanus	11.3	17.9	19.1	16.2
Hydnobolites	15.1	7.5	6.4	9.6
Hysterangium spp. 2	5.7	6.0	8.5	6.6
Hysterangium spp. 3	0.0	7.5	12.8	6.6
Rhizopogon	5.7	9.0	4.3	6.6
Gauteria		6.0	12.8	6.0
Melanogaster	11.3	1.5	2.1	4.8
Elaphomyces oreoides	5.7	4.5	2.1	4.2
Hydnotrya tulasnei	3.8	6.0	2.1	4.2
Leucogaster	0.0	6.0	4.3	3.6
Endogone pisiformis	1.9	1.5	4.3	2.4
Hysterangium spp. 1			8.5	2.4
Tuber		1.5	4.3	1.8
Genea		3.0		1.2
Mushroom				
Unknown 1	41.5	47.8	70.2	52.1
Boletaceae	5.7	22.4	25.5	18.0
Unknown 2	26.4	11.9	10.6	16.2
Russulaceae 1	11.3	13.4	21.3	15.0
Russulaceae 3	9.4	13.4	14.9	12.6
Russulaceae 2	9.4	7.5	6.4	7.8
Cortinarius	5.7	1.5	6.4	4.2
Entoloma		3.0	2.1	1.8

Table 2.3. Best mixed effects models for predicting species-specific truffle and mushroom biomass (biomass of *Elaphomyces* spp. were log transformed). Coefficients for predictor variables and their associated standard error are shown under fixed effects. Standard error due to grid, station, and residual are shown under random effects. Note that residual standard error varies by forest type. Terms included in the model are considered important based on AIC scores from backward model selection. Basal area of balsam fir, basal area of beech, distance to stream, and slope were not important predictors for any species and were not included in the table.

Model components	Truffle						Mushroom
	E. verruculosus	*E. macrosporus*	*E. americanus*	*E. bartlettii*	*H. cubispora*	*T. shearii*	All taxa
Fixed effects							
Intercept	0.847 (0.121)	0.240 (0.040)	0.163 (0.042)	0.023 (0.010)	0.009 (0.003)	0.005 (0.001)	0.601 (0.108)
Hemlock	0.546 (0.075)	0.237 (0.034)	—	0.042 (0.008)	—	—	—
Red spruce	—	—	-0.046 (0.025)	-0.013 (0.008)	—	—	—
Yellow birch	—	—	—	0.003 (0.002)	—	—	—
DWD^3	—	—	—	0.016 (0.007)	—	0.006 (0.002)	—
Leaf litter	-0.103 (0.064)	0.048 (0.023)	—	—	—	-0.002 (0.001)	—
DOY	0.604 (0.396)	—	0.621 (0.261)	—	0.076 (0.034)	0.002 (0.001)	6.483 (1.412)
DOY^2	-0.641 (0.396)	—	-0.597 (0.260)	—	-0.080 (0.034)	—	-6.386 (1.411)
Random effects							
Grid	0.128	0.008	0.015	<0.001	—	—	—
Station	0.354	0.055	0.022	<0.001	—	—	—
Residual							
Hardwood	0.296	0.156	0.378	0.021	0.005	<0.001	2.187
Mixed	1.891	0.654	0.25	0.172	0.007	0.008	3.959
Softwood	2.756	0.631	0.297	0.036	0.004	0.012	4.018

Table 2.4. Results of multiple regression analyses showing the effects of forest type and time on truffle richness from field surveys and eastern chipmunk scat. The effect of mixed and softwood forest is relative to hardwood forest. Bolded *P*-values denote statistically significant variables at $\alpha = 0.05$.

Model components	Field survey				Scat analysis			
	Coefficient	se	t	*P*	Coefficient	se	t	*P*
Intercept	2.887	1.038	2.782	**0.008**	-3.588	1.057	-3.396	**0.001**
Mixed forest	1.249	0.411	3.043	**0.004**	0.596	0.256	2.326	**0.021**
Softwood forest	1.062	0.411	2.587	**0.013**	0.481	0.279	1.721	0.087
Time (Day of year)	-0.001	0.005	-0.200	0.842	0.034	0.005	6.358	< **0.001**

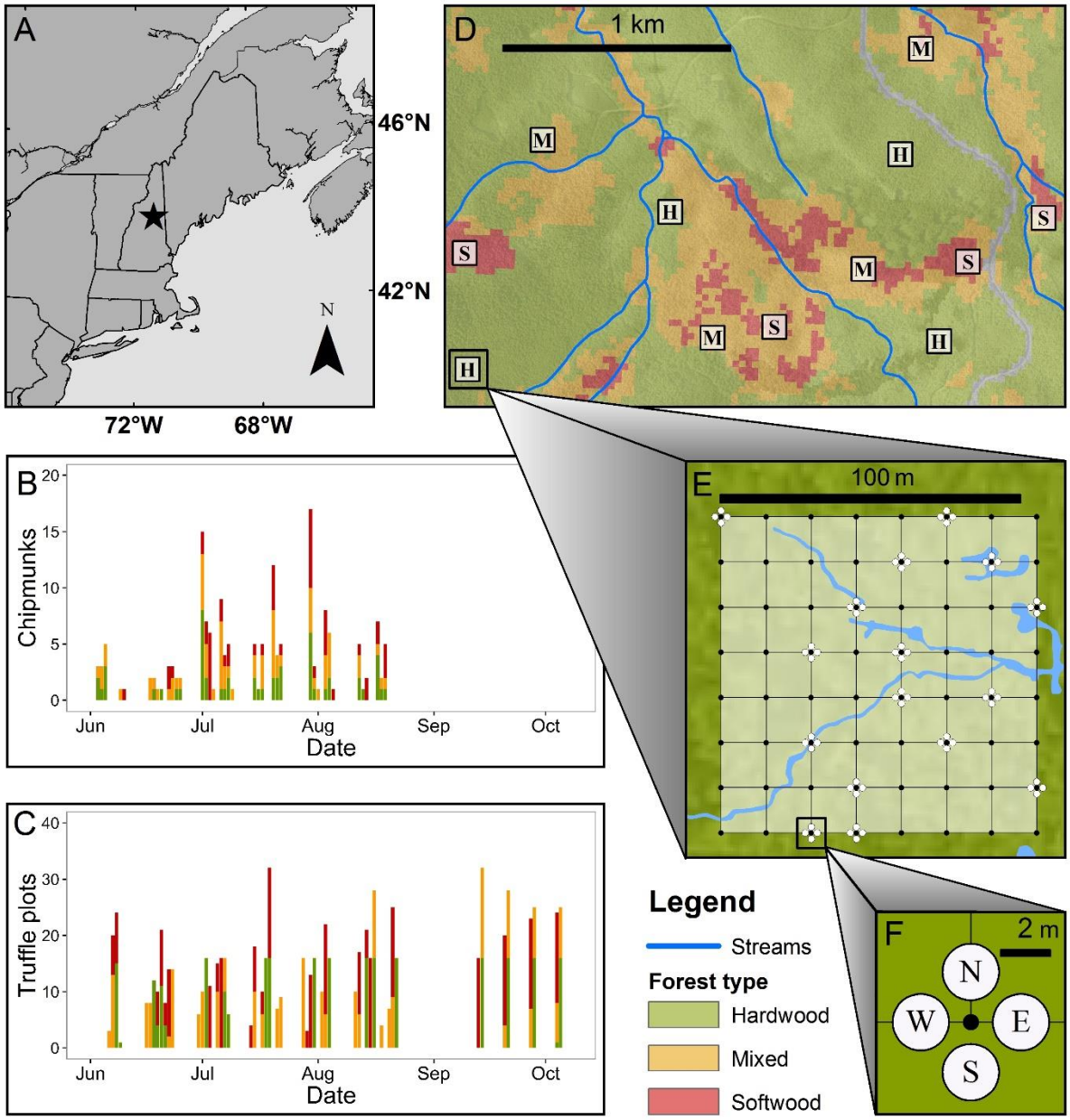


Figure 2.1. Location of grids used to sample sporocarps and eastern chipmunks at Bartlett Experimental Forest, New Hampshire, USA (A, D). A total of 12 grids consisting of an 8 x 8 station arrangement (64 total stations) was stratified across hardwood (n = 4), mixed (n = 4), and softwood (n = 4) forests (D, E). Within each of the eight grid columns, two stations were randomly selected for a total of 16 stations for sporocarp surveys (E). From each of these 16 stations, four sporocarp sampling plots were established in cardinal directions 2 m from the station center and one randomly sampled in June, July, August, or September/early October for a total of 64 plots sampled per grid and 768 plots across all grids (F, C). Eastern chipmunks were trapped on each grid with Sherman live traps set at each of the 64 stations in June, July, and August. Scat samples were collected from individual chipmunks upon first capture within a month for a total of 167 scat samples (B).

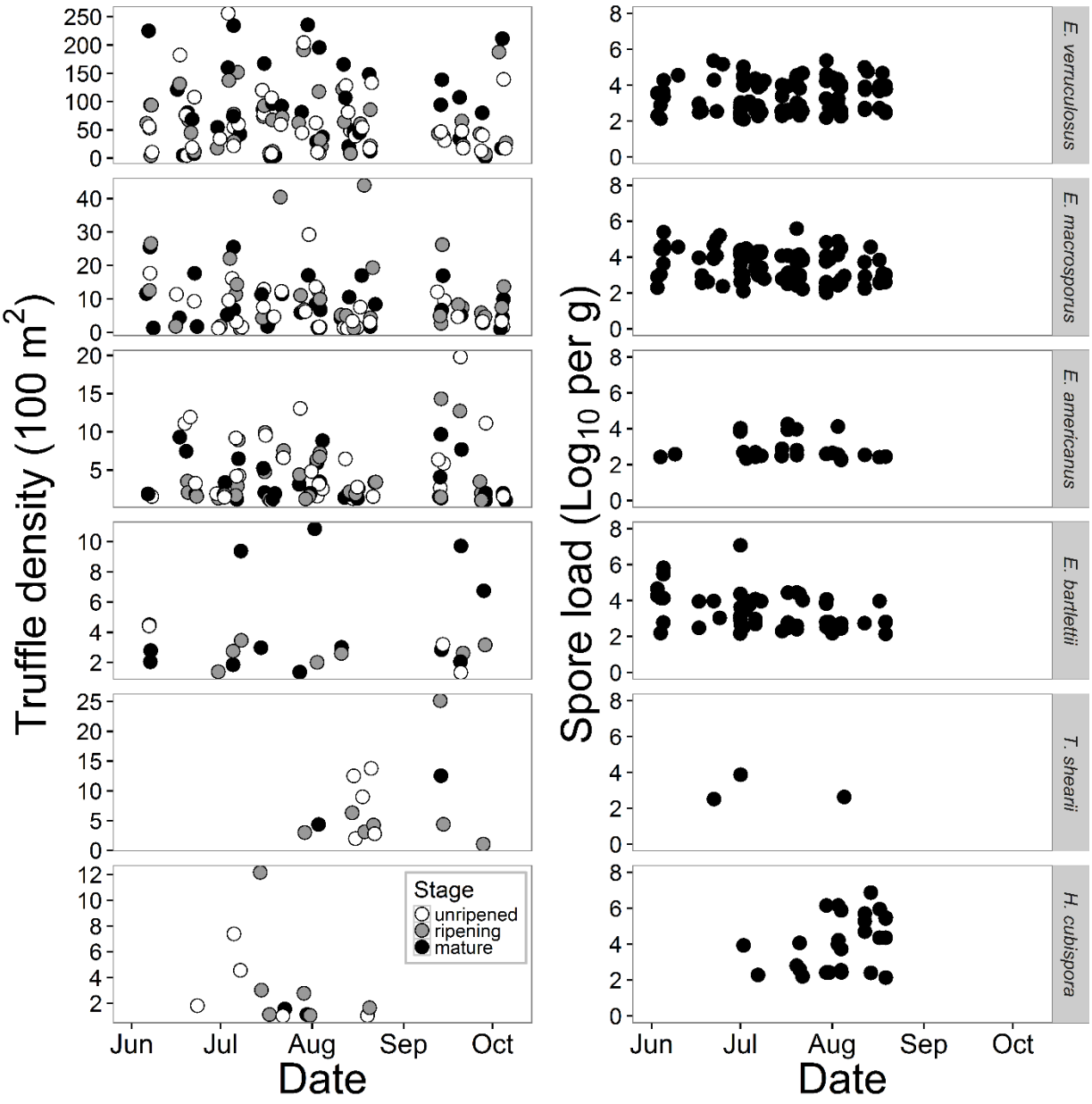


Figure 2.2. Comparison of the occurrence and relative abundance of the six most common truffle species observed in field surveys (left, n = 768) and spores in eastern chipmunk scat samples (right, n = 167). Sporocarps were collected from June through early October and scat was collected from June through mid-August. Stage of sporocarps refers to no spore formation in gleba (unripened), asci formed but many spores not mature (ripening), spores mature (mature). Sporocarp density was calculated by pooling the number of each stage within a species across a grid and standardizing to a 100 m2 area.

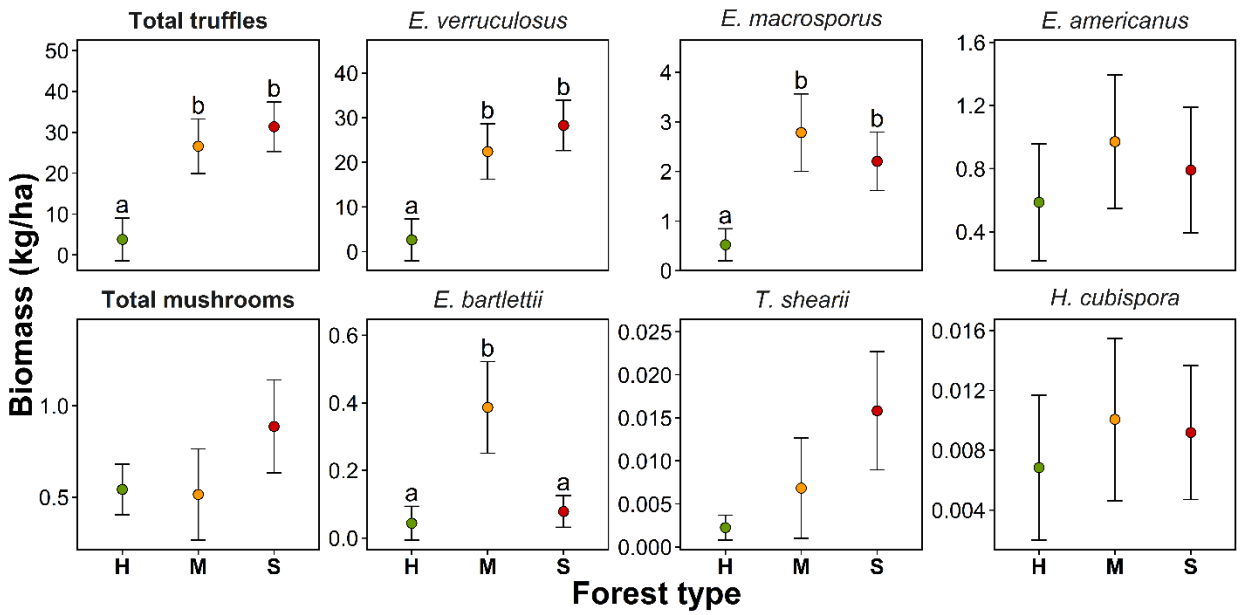


Figure 2.3. Mean biomass (kg/ha) of total truffle standing-crop, total mushroom standing-crop, and the six most common truffle species among hardwood (H), mixed (M), and softwood (S) forest types from field surveys. Bars indicate standard error. Species are arranged from the most abundant on the upper left to the least abundant on the bottom right. Within taxa, forest types sharing a common letter were not significantly different ($P < 0.05$) as indicated by mixed effects models and Tukey's post hoc tests using log transformed biomass data.

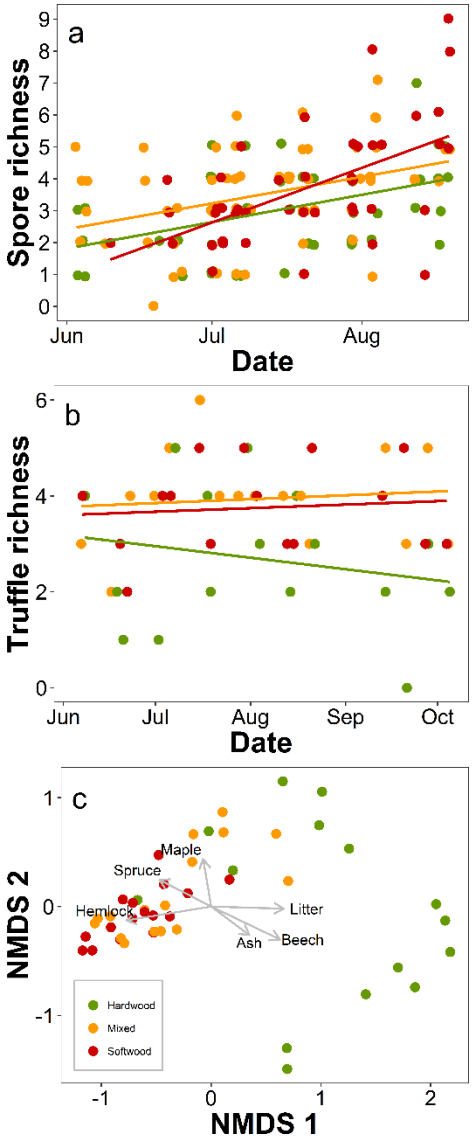


Figure 2.4. Richness of truffle spores in eastern chipmunk scat samples from June through mid-August (A), richness of truffle species fruiting from field surveys (B), and a two-dimensional nonmetric multidimensional scaling (NMDS) ordination of truffle communities based on sporocarp abundance from field surveys (C). Fitted vectors of the environmental variables indicate the direction (increasing) of the environmental gradient with length proportional to correlation with the NMDS ordination. Only significant (envfit, $P < 0.05$) environmental variables are shown: basal area of white ash (Ash), basal area of American beech (Beech), basal area of eastern hemlock (Hemlock), leaf litter depth (Litter), basal area of red maple (Maple), and basal area of red spruce (Spruce). Corresponding envfit statistics can be found in Table C1 of Appendix C. For both sporocarp richness and the NMDS ordination, sporocarps were aggregated at the grid level within a sampling period. The corresponding multiple regression analyses showing the effects of forest type and time on truffle fruiting richness based on scat (A) and field surveys (B) are shown in Table 2.4.

CHAPTER 3

PULSED RESOURCE AVAILABILITY CHANGES DIETARY NICHE BREADTH AND PARTITIONING BETWEEN GENERALIST RODENT CONSUMERS[3]

Abstract

Pulsed food availability can influence the dietary niches of consumers and modify their interspecific interactions. We used natural pulses of mast-fruiting of American beech (*Fagus grandifolia*) to test whether optimal foraging or competition structure the dietary niche breadth and overlap among two congener rodent species (*Peromyscus leucopus* and *P. maniculatus*), both of which are generalist consumers. We reconstructed diets seasonally over a two year period using stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) of hair and potential dietary items and measured both intraspecific dietary niche breadth and interspecific niche overlap using standard ellipse area calculated within a Bayesian framework. Changes in niche breadth were generally consistent with predictions of optimal foraging theory, with both species consuming more beech nuts (a high quality food resource) and having a narrower niche breadth during masting seasons compared to non-masting seasons. In contrast, changes in niche overlap were consistent with competition theory, with higher niche overlap during masting seasons than during non-masting seasons. Overall, dynamics in niche breadth and overlap were closely tied to beech masting, underscoring the need to consider food availability when investigating competition. Our findings may explain why previous studies on resource use and niche partitioning between *P. leucopus* and *P. maniculatus* have been equivocal.

[3]Ryan B. Stephens, Erik A. Hobbie, Thomas D. Lee, and Rebecca J. Rowe

Introduction

Systems with pulsed resource availability experience a natural manipulation of high quality food resources (Yang et al. 2008) and offer an opportunity to investigate the mechanisms which structure the niches of species (e.g., Stapp and Polis 2003, Selva et al. 2012, Correa and Winemiller 2014). In terrestrial ecosystems, one of the most common resource pulses is masting (or mast-fruiting), in which trees of the same species synchronously produce large seed crops in the same season, followed by an extremely low crop the next year (Ostfeld and Keesing 2000). For consumers, particularly rodents, masting events produce a food source that is not only highly abundant and energy-rich, but also easily harvested, stored, and defended (Vander Wall 2010, Cramer 2014). During non-masting years, rodents that would otherwise consume seeds must find alternative food sources, such as fungi, which although readily available are relatively low in nutrient content (Cork and Kenagy 1989, Fletcher et al. 2010).

The white-footed mouse (*Peromyscus leucopus noveboracensis*) and woodland deer mouse (*P. maniculatus gracilis*) are abundant rodents that are syntopic throughout forests in the Midwest and eastern North America (Wolff et al. 1985). Both species respond numerically to masting (Elias et al. 2004, Falls et al. 2007) and have long been used as models for studying resource use (Davidson and Morris 2001, Shaner et al. 2007) and competition (Dooley and Dueser 1990) because they are both dietary generalists and have similar morphology and habitat affinities (Wolff 1996a, Stephens et al. 2014). To understand the mechanisms which structure niche breadth and overlap among closely related species, we monitored the seasonal diets of *P. leucopus* and *P. maniculatus* in a temperate forest which had two masting events of American beech (*Fagus grandifolia*). We used stable isotope analysis of hair to measure intraspecific dietary niche breadth and interspecific dietary niche overlap and test the contrasting predictions

of optimal foraging theory (MacArthur and Pianka 1966, Perry and Pianka 1997) and competition theory (MacArthur and Levins 1967, Abrams 1983).

Optimal foraging theory states that niche dynamics are driven by the availability of food resources (MacArthur and Pianka 1966). As preferred resources become available, individuals are expected to increase dietary specialization (i.e., decrease dietary niche breadth) and as preferred resources decrease, diets will become less specialized (i.e., increase dietary niche breadth; Macarthur and Pianka 1966; Fig. 3.1A). Optimal foraging theory also predicts that although space use may be influenced by interspecific competition, diet is independent of other species (Fig. 3.1B). In contrast, competition theory predicts that, for ecologically similar species, coexistence is achieved through niche partitioning (Schoener 1974, Abrams 1983). Niche partitioning is predicted to be greatest under low resource availability, when species focus on the resource they can best extract, which decreases the diversity of food items in their diets (i.e., decreased dietary niche breadth; Schoener 1982, Bolnick et al. 2010; Fig. 3.1A) and reduces interspecific dietary similarity (i.e., niche overlap; Fig. 3.1B). During times of high resource availability, niche breadths expand and greater niche overlap can occur because resources no longer limit coexistence (Schoener 1982; Fig. 3.1A & B).

Based on these assumptions, under optimal foraging theory we predicted that both *Peromyscus* species should show similar patterns of niche overlap, irrespective of masting, and have reduced niche breadths during masting seasons compared to non-masting seasons (Fig. 3.1C). In contrast, under competition theory we predicted that, relative to non-masting seasons, both niche overlap and breadth would be high during masting seasons when food resources are not limiting and competition is reduced (Fig. 3.1D).

Methods

Study system and sample collection

We trapped small mammals and collected food items for isotopic analysis on 12 sampling grids at the Bartlett Experimental Forest, White Mountain National Forest, New Hampshire (44° 3′ 7.2″ N, 71° 17′ 25.1″ W). Grids were in hardwood (*n* = 4), mixed (*n* = 4), and softwood (*n* = 4) forest stands at 250-450 m elevation. Grids consisted of an 8 × 8 station array with 15 m spacing (64 stations; 1.1 ha) and averaged 1.23 km apart (range 0.28 - 2.61). Hardwood grids were dominated by red maple (*Acer rubrum*) and American beech (*Fagus grandifolia*) with a lesser component of sugar maple (*A. saccharum*), yellow birch (*Betula alleghaniensis*), and white ash (*Fraxinus americana*), whereas softwood grids were dominated by eastern hemlock (*Tsuga canadensis*) and red spruce (*Picea rubens*). Mixed grids had both hardwood and softwood species. Shrub cover ranged from depauperate to abundant and was primarily composed of hobblebush (*Viburnum lantanoides*); ground cover was lacking except in wet areas where sedges and ferns were common.

Small mammals were captured on each trapping grid using Sherman live traps baited with a bird seed mix and insulated with polyester batting. Traps were set within 1.5 m of each station and checked twice daily (morning and afternoon) for four consecutive days in June, July, and August of 2014 and 2015. This summer trapping was part of a broader study on small mammal ecology. Supplementary trapping was carried out in September or October of both years to collect fall hair samples for isotopic analysis. Captured *Peromyscus* were measured, weighed, sexed, aged (based on pelage color and reproductive status: juvenile, subadult, or adult), and assigned a uniquely numbered ear tag (model 1005-1; National Band and Tag Company, Newport, Kentucky, USA). *Peromyscus leucopus* and *P. maniculatus* were differentiated based on measurements, particularly ear length (Stephens et al. 2014), and questionable individuals were

confirmed using genetic analyses. For isotopic analysis, we collected approximately 1 to 4 mg of hair from the dorsal posterior of an individual upon first capture and only took additional hair samples if molting occurred between trapping periods. We used the number of *Peromyscus* captured on a grid between June – August as a general index for abundance within years. The trapping protocol was approved by the University of New Hampshire Animal Care and Use Committee (protocol 140304) and followed guidelines outlined by the American Society of Mammalogists (Sikes et al. 2016).

For isotopic analysis of the resource base, we collected six potential food sources known to comprise the majority of dietary items of *P. leucopus* and *P. maniculatus*: beech nuts, red maple seeds, ectomycorrhizal (EM) fungal sporocarps, arbuscular mycorrhizal (AM) fungal sporocarps, berries, and arthropods (Linzey and Linzey 1973, Wolff et al. 1985). Beech nuts, red maple seeds, and berries (hobblebush and partridge berries [*Mitchella repens*]) were collected opportunistically while trapping. Arthropods were collected using small pitfall traps and were analyzed at the order level: beetles (Coleoptera), grasshoppers (Orthoptera) and spiders (Araneae). The EM sporocarps (genus *Elaphomyces*) were collected as part of a companion study (Stephens et al. 2017) and AM sporocarps (primarily *Glomus* spp.) were taken from the stomachs of five woodland jumping mice (*Napaeozapus insignis;* > 70% fungi by volume) because they are too small to be detected with field surveys (Stephens et al. 2017). *Napaeozapus insignis* were collected at Bartlett Experimental Forest during the summer of 2015 by the US Forest Service (USFS). Individual samples within a dietary item were aggregated at the grid level to form a composite grid sample, with the exception of EM and AM fungi for which samples were analyzed individually.

Beech masting

Beech masting events tend to be highly variable across time, often separated by several years (Cleavitt and Fahey 2017). However, during the fall months of 2013 and 2015, Bartlett Experimental Forest experienced two masting events which were interceded, in the fall of 2014, by an extremely low beech nut crop. Masting is driven by climatic variables and is synchronized across regions, even at locations separated by up to 1000 km (Koenig and Knops 1998, Piovesan and Adams 2001). Data from nearby Hubbard Brook Experimental Forest (ca 40 km away) confirmed our observations at Bartlett Experimental Forest and indicated that beech nut availability was over an order of magnitude higher during 2013 and 2015 (39.1 seeds/m^2 and 33.1 seeds/m^2, respectively) than during 2014 (2.4 seeds/m^2; Cleavitt and Fahey 2017). During masting years, nuts are cached by *Peromyscus* spp. (Wolff 1996b) and consumed through the summer of the following year. As such, our high mast seasons were summer 2014 and fall 2015, whereas our low mast seasons were fall 2014 and summer 2015. Although beech trees were not distributed evenly among hardwood, mixed, and softwood forest types (average basal area [m^2/ha] of 13.4, 2.9, and 1.9, respectively), all grids contained trees capable of producing mast (Leak and Graber 1993), with at least 12 beech trees/ha that were ≥ 10 cm in diameter and at least two trees/ha that were ≥ 30 cm. *Peromyscus* also will travel over 120 m to collect food items and can store over 8 liters of husked beech nuts (Hamilton 1941), further suggesting that beech nuts were available to individuals on all grids.

Other common mast producers in our study area included eastern hemlock, red spruce, and red maple. At Bartlett Experimental Forest, eastern hemlock and red spruce masted in the fall of 2013 and 2015 and red maple masted in the spring of 2014 and 2015. Based on data from Hubbard Brook (at similar elevations to our sites), red maple seeds were over 5 times more abundant during the summer

of 2015 compared to the summer of 2014 (Nick Rodenhouse; personal communication). However, despite masting of these tree species, their seeds are likely not a preferred food source. Rodents select seeds which are energy- and nitrogen-rich, easy to collect, and large in size (Jensen 1985). Relative to seeds from other tree genera, beech nuts have more calories per gram (Grodziński and Sawicka-Kapusta 1970, Jensen 1985) and are easy to collect as they are concentrated near the tree trunk from barochory dispersal (gravity), rather than scattered across the forest floor by the wind (Hughes and Fahey 1988, Wagner et al. 2010). Additionally, excluding the inedible seed coats, beech nuts on our grids (168.8 mg, $n = 25$) were 20 times larger than red maple seeds (8.5 mg, $n = 75$) and 75 times larger than red spruce seeds (2.3 mg, $n = 25$) or eastern hemlock seeds (2.2 mg; $n = 25$).

Stable isotope measurement

Hair samples were soaked in 2:1 chloroform:methanol for 24 hours to remove surface oils, after which they were re-rinsed, air dried, and cut into small pieces. Food items were rinsed with 2:1 chloroform:methanol and ground to a fine powder. Hair samples (1 mg) and food items (1 – 5 mg) were weighed into tin capsules and analyzed for stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes and elemental composition (%C, %N) at the University of New Hampshire Stable Isotope Lab using an Elementar Americas Pyrocube elemental analyzer coupled to a GeoVision isotope ratio mass spectrometer. Raw $\delta^{13}C$ and $\delta^{15}N$ values were adjusted based on a 3-point normalization using in-house standards. Isotopes are expressed in delta (δ) notation as parts per thousand (‰) deviation from the standard using the formula:

$$\delta = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and standards are Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric N_2 ($\delta^{15}N$). Measurement precision based on repeated analyses of in-house standards

was ± 0.1 ‰ for $\delta^{13}C$ and ± 0.2 ‰ for $\delta^{15}N$. To capture an isotopic signal from the general population and avoid an individual grid from biasing our results, we used up to nine hair samples per species from a grid within a season.

Stable isotope integration period and values

Unlike other animal tissues (e.g., muscle or liver) which turn over continuously, hair is metabolically inactive and integrates an isotopic signature of diet at the time of growth (Dalerum and Angerbjörn 2005). Thus, the isotopic signature of diet from hair may be offset from the collection time and an understanding of molting ecology is required to determine the temporal window of integration (Fraser et al. 2013). In *Peromyscus* spp., individuals go through both ontogenetic and seasonal molts. Young of the year molt from juvenile to sub-adult pelage and again from sub-adult to adult pelage. Depending on the time of birth, these ontogenetic molts take place either during the summer or fall and can take as little as 10 days to complete (Gottschang 1956, Tabacaru et al. 2011). Adult *Peromyscus* generally have two seasonal molting periods, one in early summer following the breeding season and one in the fall (Brown 1963, Tabacaru et al. 2011). Because ontogenetic molts are characterized by changes in hair color and seasonal molts by changes in both hair color and hair length (Collins 1923), we could bin hair samples into distinct summer and fall seasons for both years. Methods used to construct bins are detailed in Appendix D.

Seasonal bins are appropriate because hair records an isotopic signature of diet during hair growth and molting peaks in the early summer and fall. However, in some instances, young of the year may have grown hair spanning both the summer and fall seasons. To ensure that this did not influence our results, we identified and removed outliers within seasons that indicated a mismatch

in the diet signal compared to the rest of the population. For both species, within each season, we checked for multivariate outliers of $\delta^{15}N$ and $\delta^{13}C$ using the adjusted quantile method of 'aq.plot()' in the R package 'mvoutlier' (R Development Core Team 2016, Filzmoser and Gschwandtner 2017).

Prior to our niche analyses, we identified factors influencing $\delta^{15}N$ and $\delta^{13}C$ values (and their spread) using linear mixed effects models in 'lme' from the R package 'nlme' (Pinheiro et al. 2012). Fixed effects included species (*P. leucopus* and *P. maniculatus*), season (summer and fall), masting phase (masting and non-masting), and forest type (hardwood, mixed, and softwood). For random effects, we considered both a random intercept of year (to account for between-year variation) and grid within year (to account for between-grid variation within a year). For spread we considered a multiple variance structure that allowed residual error to vary by season, masting phase, or forest type. The random intercept (year or grid nested within year) and the multiple variance components were sequentially compared with the final random effects structure selected using Akaike's information criterion (AIC) and a likelihood ratio test. Model fit was assessed by plotting residuals versus fitted values and by evidence of homogeneity of variances and normality of both the residuals and random effects (Zuur et al. 2009).

Dietary composition and niche analyses

Our mixed effects models indicated that forest type had no significant effect on $\delta^{15}N$ or $\delta^{13}C$ values (see results), and preliminary analyses confirmed similar patterns among forest types. Therefore, we combined forest types for all analyses, giving a sample size of ≥ 24 for all groups, which is recommended for robust isotopic niche estimates and reduced uncertainty surrounding them (Syväranta et al. 2013).

We assessed the diets of *P. leucopus* and *P. maniculatus* using Bayesian stable isotope mixing models in the R package 'MixSIAR' (Stock and Semmens 2013). *MixSIAR* uses $\delta^{15}N$ and $\delta^{13}C$ values from both consumer tissues (i.e., hair) and each food source along with discrimination factors, elemental concentrations, and the uncertainties surrounding those values to calculate the relative proportion of food sources consumed. We used separate models for species in each season and year; running each model with three chains for 200,000 iterations, removing the first 50,000 and thinning by 50, resulting in 9,000 draws of the posterior distribution.

For all mixing models we used informative priors which improve precision and accuracy (Moore and Semmens 2008). For an individual food source, priors were scaled by the relative proportion of weeks it was available during a season (Fig 3.2). Temporal availability was based on phenology recorded in the literature, food sources observed in the field, and through microscopy of scat. During a masting year, we considered beech nuts to be available from the fall mast into the summer of the following year, whereas during a non-masting year they were only available for a one week period in mid-October (corresponding to peak nut fall) and were unavailable (α prior set to 0.01) the following summer (Leak and Graber 1993, Wolff 1996a). Red maple seeds are available during late spring through early summer (Houle 1994), with most seeds removed within 1 - 2 months (Myster and Pickett 1993). EM sporocarps (Stephens et al. 2017), berries (Gervais and Wheelwright 1994), and arthropods are available year round, whereas AM sporocarps are primarily consumed during summer. For the food source parameters of $\delta^{15}N$ and $\delta^{13}C$, we used means and standard deviations of collected food items and accounted for differences in elemental concentrations.

Consumer tissues are enriched in ^{13}C and ^{15}N relative to food sources and to put them into consumer isospace they must be adjusted. We calculated isotopic enrichment factors for natural diets at Bartlett Experimental Forest of 1.92 for $\delta^{15}N$ and 4.64 for $\delta^{13}C$ using stomach contents (bulk diet) and hair samples collected from *P. maniculatus* during the summer of 2015. During this time, the diets of *P. maniculatus* were highly constrained (Fig. 3.3), allowing us to minimize effects from intraspecific variation. Stomach samples were taken from individuals (n = 9) collected in hardwood forest by the USFS and hair samples were taken from *P. maniculatus* live trapped in hardwood forest (n = 11). We used large standard deviations of 1.0‰ for $\delta^{15}N$ and 2.3‰ for $\delta^{13}C$ to account for any uncertainty surrounding our discrimination factors.

We compared the isotopic niche breadth and overlap of *P. leucopus* and *P. maniculatus* among seasons and years using the R package 'SIBER' (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011). Using a Bayesian MCMC algorithm, *SIBER* combines the prior probability with the likelihood of the data to generate a distribution of the covariance matrix to calculate standard ellipse area (SEA; expressed as $‰^2$). The SEA represents the core isotopic niche space occupied by a species and is robust to differences in sample size. We assessed shifts in the shape and location of the isotopic niche breadth and overlap using SEA_c (estimated from maximum likelihood and corrected for small sample size). Additionally, we quantitatively compared niche breadth and overlap in each season and year using Bayesian Standard Ellipse Area (SEA_b) and calculated the probability that the posterior distributions of one group was different from another group. We considered a probability > 0.90 to reflect important differences in the size of the niche breadth or the amount of niche overlap. For both models, we ran three chains for 200,000 iterations, removed the first 50,000, and thinned by 50, resulting in 9,000 posterior draws of the covariance matrix to construct ellipses.

Results

More *P. leucopus* and *P. maniculatus* were captured in the high-mast summer (2014) than in the following low-mast summer (2015), although the decline was much less dramatic for *P. leucopus* (9.2 ± 5.2 to 6.8 ± 3.5) than for *P. maniculatus* (30.2 ± 18.6 to 10.2 ± 6.7). In total, we collected 263 *P. leucopus* hair samples (126 in 2014 and 137 in 2015) and 650 *P. maniculatus* hair samples (455 in 2014 and 195 in 2015). We used up to nine hair samples per species from a grid and season, resulting in 180 *P. leucopus* and 195 *P. maniculatus* hair samples with stable isotope values. Analysis of multivariate isotopic outliers resulted in the removal of five *P. leucopus* and six *P. maniculatus* for a total of 175 *P. leucopus* (within each season and year: average 43.8; range 24 to 59) and 189 *P. maniculatus* (average 47.3; range 37 – 63) hair samples (Fig. 3.3). *Peromyscus* species, season, and masting phase all significantly influenced $\delta^{15}N$ and $\delta^{13}C$ values, whereas forest type did not (Table 3.1). Compared to season and forest type, masting phase had the largest influence on residual spread of $\delta^{15}N$ and $\delta^{13}C$ values, with 3.2 and 4.2 times more variability, respectively, during the non-masting phase than the masting phase.

The potential food sources had distinct $\delta^{15}N$ and $\delta^{13}C$ values (Fig. 3.2A). Although beech nuts and AM sporocarps were close in isotopic space, they were largely available in different seasons (Fig. 3.2B), making it possible to distinguish between them in the mixing models. Differences in $\delta^{15}N$ and $\delta^{13}C$ between the *Peromyscus* species, season, and masting phase were reflected in the food items consumed (Fig. 3.3). During beech masting, the diets of *P. leucopus* and *P. maniculatus* were nearly identical, with the diet comprised primarily of seeds or nuts (50 – 62%) and approximately a third coming from beech nuts alone (28 – 34%; Fig. 3.3). During non-masting phases, diets varied widely and beech nuts contributed very little (0 – 7%). In the first low beech mast season (Fall 2014), *P. leucopus* tended to consume more berries (26% vs

15%) and arthropods (25% vs 17%) and less red maple (9% vs 21%) and AM fungi (11% vs 22%) than *P. maniculatus*. Overall consumption of fungi was approximately two times higher during the non-masting fall of 2014 compared to the masting fall of 2015 for both *P. leucopus* (34% vs 20%) and *P. maniculatus* (40% and 18%). During the second low beech mast season (summer of 2015), when red maple masted, both species consumed red maple seed, but in different relative proportions; red maple only comprised 34% percent of the diet for *P. leucopus* while it was the majority of the diet for *P. maniculatus* (56%). Additionally, during the summer of 2015, berries contributed about five times more to the diet of *P. leucopus* (17%) than to *P. maniculatus* (3%). Consumption of arthropods was relatively consistent across seasons and years for both *P. leucopus* (17 - 19% of diet) and *P. maniculatus* (15 - 18%), with the exception of *P. leucopus* during the fall of 2015 (25%).

Changes in the size and location of the isotopic niches of *P. leucopus* and *P. maniculatus* were associated with masting phase and influenced by both $\delta^{15}N$ and $\delta^{13}C$ values (Table 3.1, Fig. 3.3, Fig. 3.4). For both species, niche breadth (SEA_b) was generally 3 - 5 times larger during non-beech masting seasons (4.1 to 6.3‰^{2}) compared to beech masting seasons (1.2 to 1.9‰^{2}). The exception to this was *P. maniculatus* during the low beech mast summer of 2015 (while red maple seed availability was high) when its SEA_b (1.4‰^{2}) resembled that of the beech masting summer of 2014 (1.2‰^{2}). Despite larger niche breadths during non-masting seasons, niche overlap (SEA_b overlap; 4 – 33%) was generally less than half of that observed during beech masting seasons (57 – 73%).

Discussion

Without manipulative experiments, assessing the role of foraging behavior and interspecific competition in structuring diet can be challenging due to difficulty in quantifying

the use of limiting resources (Schoener 1974, Perry and Pianka 1997). We used natural pulses of beech mast to test the opposing predictions of optimal foraging theory and competition theory for dietary niche breadth and overlap of two closely related rodents that are generalist consumers (*P. leucopus* and *P. maniculatus*). We found patterns in niche breadth generally consistent with predictions of optimal foraging theory and patterns in niche overlap consistent with competition theory.

Foraging theory posits that species will select foods that maximize energy intake and minimize handling time. Thus, species will have specialized diets when preferred resources are abundant and will broaden diets to include less profitable food items to meet dietary requirements during times of low resource availability (MacArthur and Pianka 1966, Perry and Pianka 1997). Our results support optimal foraging theory with a narrowing of the dietary niche breadth of both species during seasons of high beech mast availability. During low beech mast availability, niche breadths generally expanded along with corresponding increases in fungal consumption, a food source of low nutritional value. For both species, arthropod consumption was relatively stable throughout the study and likely reflected the high protein content of arthropods relative to either seeds, fungi, or berries. Thus, arthropods were a complementary resource, supplying protein requirements while seeds, fungi, and berries provide energy (Shaner et al. 2007).

Competition theory predicts that niche overlap between ecologically similar species should be highest when resources are abundant and lowest when resources are limited, allowing species to coexist during times of low resource availability (Schoener 1982, Chesson 2000). Our results support this prediction with high dietary niche overlap during times of beech masting and low niche overlap when beech mast was not available. This finding may explain why these

species often co-occur with little spatial or habitat segregation (e.g., Wolff 1985). Similar patterns of niche overlap have been observed in other rodents consuming tree mast in Poland and the western United States (e.g., Selva et al. 2012, Reid et al. 2013). One prior study investigated the diets of wild syntopic *P. leucopus* and *P. maniculatus*. Using analysis of stomach contents from mice collected during peak *Peromyscus* density (when competition should presumably be highest), Wolff et al. (1985) concluded that these species had similar diet habits but likely did not compete for food. However, samples were collected the year following an oak masting event (*Quercus* spp.; Wolff 1996), when food resources were likely not limiting. Similar to Wolff et al. (1985), dietary overlap was high during the summer following beech masting when mast was still available in caches and *Peromyscus* densities were at their peak. In contrast, when *Peromyscus* densities were low during the non-masting summer of 2015, niche partitioning was high, suggesting that competition was higher during this time. Thus, high consumer densities are not always reliable indicators of competition. Our results suggest that competition is driven by food shortages which are often reflected by lower consumer densities. During years of extremely low *Peromyscus* densities, we may expect that interspecific competition is relaxed because basic food requirements are easily met.

Patterns of niche breadth were variable for *P. maniculatus* during periods of low beech mast availability. While its niche expanded during the first low mast period (fall 2014), a response consistent with optimal foraging theory, its niche contracted during the second low mast period (summer 2015), consistent with competition theory. This later niche contraction was during high red maple seed availability and may reflect differences in foraging strategies between the two *Peromyscus* species. Experimental feeding trials by Cramer (2014) suggest that *P. maniculatus* may be a seed specialist whereas *P. leucopus* is a generalist, having little preference

for seed type. Our findings support this experimental work and suggest that, compared to *P. leucopus*, *P. maniculatus* may have a lower giving-up density for red maple seeds and can capitalize on this ostensibly lower quality food source when it is highly available. This may be especially true during low population densities of *P. maniculatus* when individuals increase foraging time (Davidson and Morris 2001).

Variability in niche response to low food availability has also been documented in other systems. For example, Correa and Winemiller (2014) observed both niche expansion and niche stasis among Amazonian fish in response to reduced terrestrial subsidies. It is likely the complicated interplay between species-specific foraging behaviors and differences in availability of alternative food sources in natural communities which generate heterogeneity in patterns of niche breadth. During times of low resource availability, species may either expand their dietary niche or specialize on a single food item, depending on how much of a generalist or specialist the species is and the extent to which alternative food sources are available. Additionally, for some species, intraspecific competition may influence niche dynamics, with lower abundances leading to less individual specialization and an overall smaller species niche breadth (Svanbäck and Bolnick 2007).

Our results highlight that broad similarity among congeners may mask important differences and caution against assumptions of equivalency in ecological studies (e.g., Schnurr et al. 2002). Although the diets of both *Peromyscus* converged during times of beech masting, they diverged during seasons with low mast availability. This diet plasticity may also have important implications for changes in ecosystem function. For example, during seasons of low mast, consumption of fungal sporocarps nearly doubled. A rise in fungal consumption likely increases spore dispersal of mycorrhizal fungi which are required for tree growth and seedling establishment (Maser

et al. 1978). Dietary switching of these generalist consumers could also influence interspecific interactions with other rodent consumers, particularly those which feed on fungi. The cascading influence of niche partitioning and species interactions on ecosystem function warrants further study.

Table 3.1. Optimal mixed effects models predicting $\delta^{15}N$ and $\delta^{13}C$ values from *P. leucopus* and *P. maniculatus* hair samples. Fixed effects variables included species (*P. leucopus* and *P. maniculatus*), season (summer and fall), masting phase (masting and non-masting), and forest type (hardwood, mixed, and softwood). For each variable, the effect is relative to the one not listed (e.g., effect of *P. maniculatus* is relative to *P. leucopus*). Random intercept includes year and grid for $\delta^{15}N$ and year for $\delta^{13}C$. Both $\delta^{15}N$ and $\delta^{13}C$ models have a residual standard error structure that varies by masting phase. Bolded *P* values denote statistically significant variables at $\alpha < 0.10$.

Model components	$\delta^{15}N$					$\delta^{13}C$				
	β	SE	df	t-value	*P*-value	β	SE	df	t-value	*P*-value
Fixed effects										
Intercept	3.192	0.573	337	5.575	**<0.0001**	-22.449	0.558	357	-40.226	**<0.0001**
Species (*P. maniculatus*)	-0.510	0.104	337	-4.900	**<0.0001**	0.306	0.069	357	4.441	**<0.0001**
Season (Summer)	-0.702	0.165	337	-4.262	**<0.0001**	0.646	0.127	357	5.100	**<0.0001**
Masting phase (Non-masting)	0.770	0.149	337	5.180	**<0.0001**	-0.806	0.111	357	-7.235	**<0.0001**
Forest type (Mixed)	-0.285	0.280	20	-1.018	0.3209	0.100	0.084	357	1.195	0.2329
Forest type (Hardwood)	0.325	0.276	20	1.175	0.2537	-0.087	0.082	357	-1.057	0.2911
Random effects										
Year		0.556					0.604			
Grid		0.244					—			
Residual- Masting phase (Masting)		0.654					0.283			
Residual- Masting phase (Non-masting)		1.905					1.173			

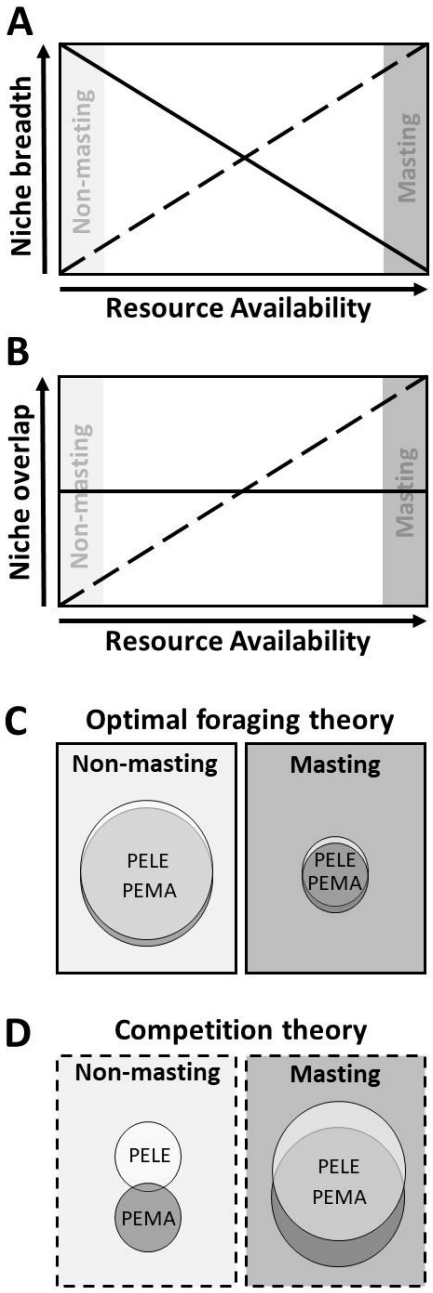


Figure 3.1. Contrasting predictions for changes in niche breadth (A) and overlap (B) based on optimal foraging theory (solid line; C) and competition theory (dashed line; D) during low resource availability (non-masting) and high resource availability (masting). Under optimal foraging theory, intraspecific niche breadth is highest during non-masting (A, C) and interspecific niche overlap for *Peromyscus leucopus* (PELE) and *P. maniculatus* (PEMA) should not differ between non-masting and masting (B, C). Under competition theory, intraspecific niche breadth and interspecific niche overlap are predicted to be lowest during non-masting and highest during masting (A, B, D).

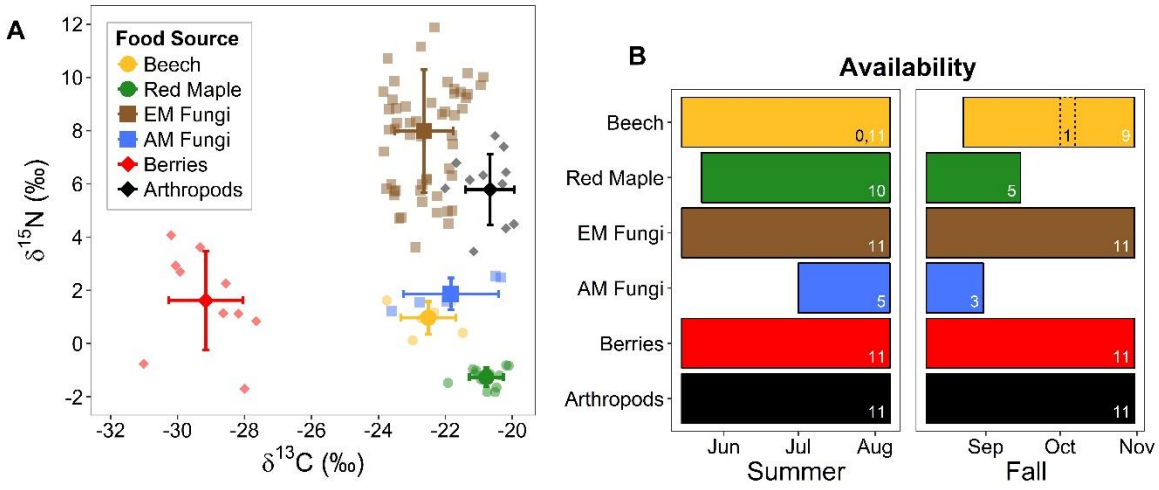


Figure 3.2. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of major food sources for *Peromyscus leucopus* and *P. maniculatus* (A). Small shapes indicate sample values (analyzed individually for EM and AM fungi and aggregated at the grid level for other food sources) and large shapes with bars indicate means and standard deviation of $\delta^{15}N$ and $\delta^{13}C$, respectively: beech nuts (1.0 ± 0.6; -22.5 ± 0.8‰; *n* = 6), red maple seeds (-1.3 ± 0.5‰; -20.8 ± 0.4‰; *n* = 12), ectomycorrhizal (EM) fungal sporocarps (8.0 ± 2.3‰; -22.6 ± 0.9‰; *n* = 56), arbuscular mycorrhizal (AM) fungal sporocarps (1.9 ± 0.6‰; -21.8 ± 1.4‰; *n* = 5), berries (1.6 ± 1.9‰; -29.2 ± 1.1; *n* = 10), and arthropods (5.8 ± 1.3; -20.7 ± 0.7‰; *n* = 12). Values of $\delta^{15}N$ and $\delta^{13}C$ have been adjusted by +1.92 and +4.64, respectively, to correct for dietary enrichment; putting food sources into the isotopic space of consumer hair. Boxes and numbers indicate the number of weeks that a food source is available during the summer and fall hair growing period (B). For beech, solid boxes and white numbers indicate the number of weeks available during a masting event and dotted boxes and black numbers indicate availability during a non-masting event.

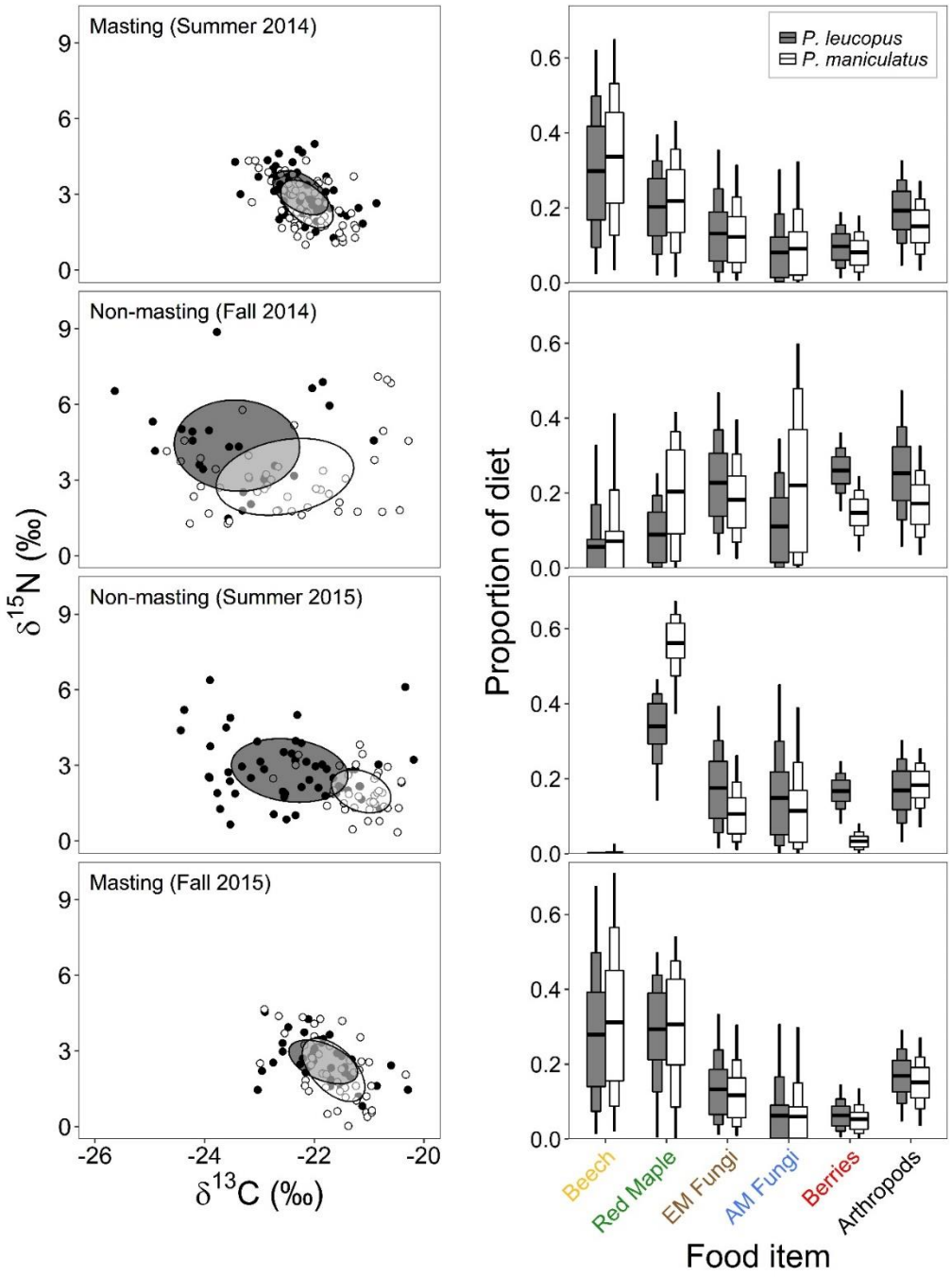


Figure 3.3. Biplots of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes (Left) and results of mixing models showing the proportion of food items contributing to the diets of *Peromyscus leucopus* and *P. maniculatus* (Right) during beech masting and non-masting phases. Circles represent hair samples of individuals (*P. leucopus* = filled; *P. maniculatus* = open) and ellipses represent the standard ellipse area corrected for small sample size (SEA_c). Medians of dietary proportions are indicated by a thick horizontal bar and Bayesian credible intervals are denoted by box width (50% thick box; 75% intermediate box; and 95% thin box). Sample sizes for *Peromyscus leucopus* and *P. maniculatus*, respectively are: summer 2014 (59, 63), fall 2014 (24, 45), summer 2015 (53, 37), and fall 2015 (39, 44).

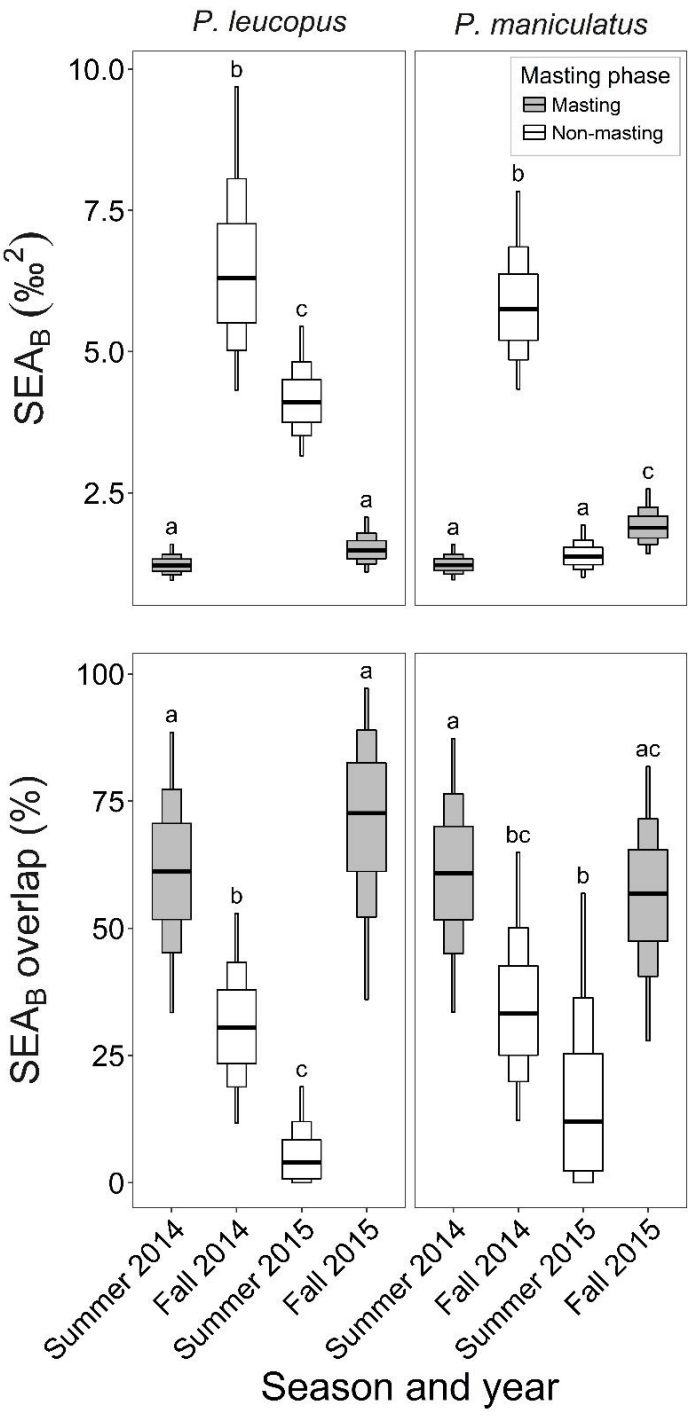


Figure 3.4. Bayesian standard ellipse area (SEA_B) (Top) and overlap (Bottom) for *Peromyscus leucopus* and *P. maniculatus* during the masting and non-masting periods. Medians are indicated by the thick horizontal bar and Bayesian credible intervals are denoted by box width (50% thick box; 75% intermediate box; and 95% thin box). Different letters between seasons indicate that the probability is > 0.90 that the larger group is greater than the smaller group.

CHAPTER 4

THE UNDERAPPRECIATED ROLE OF GENERALISTS IN RODENT-MYCORRHIZAL DISPERSAL NETWORKS[4]

Abstract

Animals are often the primary dispersers of seeds and symbiotic fungal spores. Specialist species, that consume fruits or fungal fruiting bodies as their primarily food source, are thought to play a more important role in dispersal networks compared to generalist species. However, dispersal networks are often based on occurrence data, overlooking the influence of animal abundance on a species' interactions and their dispersal effectiveness. We assessed the relative importance of specialist and generalist rodent species to dispersal of mycorrhizal fungi in temperate forests of northern New Hampshire. We tracked the interaction of five rodent species and 34 mycorrhizal taxa over a three-year period across hardwood, softwood and mixed forest stands. Using network analyses, we accounted for fluctuations in rodent abundance and differences in the mycorrhizal spore loads they dispersed. *Myodes gapperi*, a well-known fungal specialist, carried a more diverse and abundant spore community than rodent generalists and was consistently the most important disperser in its favored habitat. Nevertheless, during years when generalist species such as *Tamias striatus* and *Peromyscus maniculatus* reached high abundance, their relative importance in networks was equal to or greater than that of *M. gapperi*, particularly in forest types where *M. gapperi* was less common. Population increases of generalists were

[4]Ryan B. Stephens and Rebecca J. Rowe

coincident with the germination of tree seeds following masting, a time when inoculation by mycorrhizal fungi is critical. Our findings suggest that although specialists play key roles in rodent-mycorrhizal dispersal networks, generalists play a heretofore underappreciated role.

Introduction

Dispersal is a fundamental ecological process that exerts effects on population dynamics and is a key mechanism for structuring communities (Urban et al. 2008). In many systems, animals are the primary dispersers of plant seeds and fungal spores (Maser et al. 2008, Nathan et al. 2008). Communities composed of complex interactions between multiple animal species and the numerous plant or fungal taxa they disperse are often represented as networks, particularly for frugivorous animals dispersing plant seeds (Escribano-Avila et al. 2018). Most dispersal networks are characterized by considerable heterogeneity in species interactions, such that some animal species accumulate more interactions than others and are thus comparatively more important to the structure of the dispersal community (Bascompte et al. 2006).

Identifying the characteristics or functional traits of species that are relatively more important within dispersal networks is essential for understanding how networks function and how they may be influenced by disturbances (Sebastián-González 2017). Dietary specialization is commonly considered to be among the best predictors of a species importance within seed dispersal networks, with species that consume fruits as their primarily food source contributing the greatest to seed dispersal (Pigot et al. 2016, Sebastián-González 2017, de Assis Bomfim et al. 2018). However, species with more generalized diets may occasionally be the most effective dispersers, particularly if they can move seeds long distances (Donatti et al. 2011, Escribano-Avila et al. 2014) or if they occur in habitats not occupied by specialists (Carlo and Morales 2016).

Although abundance of animals is important in structuring species interactions (Vázquez et al. 2007, Wells et al. 2014, Winfree et al. 2015), it is often not considered when investigating the relative role of animals in dispersal networks. This is, in part, because interaction networks have traditionally been based on the presence of interactions (binary data), often referred to as qualitative networks (Pigot et al. 2016). In contrast, quantitative networks are weighted by interaction frequency and thus can incorporate the effect of animal abundance. Recently, within a plant-pollinator context, Ballantyne et al. (2015) have also accounted for the effectiveness of the mutualistic interactions by extending quantitative networks to include the quantity of propagules dispersed (e.g., number of pollen grains deposited by a pollinator). These importance networks (sensu Ballantyne et al. 2015) are likely a more realistic representation of the network structure than either qualitative or traditional quantitative networks (Schupp et al. 2010), but have yet to be applied broadly to dispersal networks.

To better understand how diet specificity, species abundance, and dispersal effectiveness influence the relative importance of animal species within dispersal networks, we developed quantitative networks (accounting for animal abundance and effectiveness of interactions) for rodents and mycorrhizal fungi across a heterogeneous forest landscape. Past studies of mycorrhizal dispersal by rodents, or other fungivorous small mammals, have used richness of fungal taxa dispersed by a species as an indicator of importance (e.g., Nuske et al. 2017; but see Schickmann et al. 2012). These studies have advanced our understanding of how animals disperse mycorrhizal fungi, but are limited in their ability to directly assess the relative importance of species within the community, particularly if abundance varies among species. Fungivorous rodents facilitate dispersal of fungi by eating mycorrhizal fruiting bodies (mushrooms or truffles) and excreting spores in their scat. Truffles fruit underground and rely

almost exclusively on small mammals such as rodents for dispersal. Rodents detect volatile compounds released by mature truffles, excavate the truffle, and consume the flesh of the fruiting body along with millions of microscopic spores (Pyare and Longland 2001). Spores pass through the digestive system unharmed (Colgan and Claridge 2002) and are dispersed to new areas through defecation. With few exceptions, truffles are produced by mycorrhizal fungi (Maser et al. 1978). These fungi colonize the roots of trees and enhance the ability of trees to access water and soil nutrients (Smith and Read 1997). This relationship is symbiotic, with the fungi receiving carbohydrates in exchange. Rodent-mediated dispersal of mycorrhizal fungi can facilitate fungal colonization of new areas and increase the local taxonomic and genetic diversity of fungal communities in forest stands. Furthermore, this dispersal can provide the mycorrhizal inoculum required for the establishment and growth of seedlings (Terwilliger and Pastor 1999, Frank et al. 2009).

Although some rodent species are fungal specialists (often referred to as obligate or preferential mycophagists), and depend on fungi as a major portion of their diet, others are opportunistic and have more generalized diets consisting of seeds, vegetation, arthropods, fruits, and fungi (Maser et al. 1978). We focused on five rodent species that differed in their consumption of fungi and recorded their interactions with mycorrhizal taxa over a three year period and among three forest types in the White Mountain region of New Hampshire. This region is characterized by marked year-to-year fluctuations in rodent abundance and is home to a rich and abundant truffle community (Stephens et al. 2017b, 2017a). We assigned rodents to dietary guilds (fungal specialist or dietary generalist) based on the amount of fungi in their diets and used scat to determine potential spore dispersal of each rodent species. We constructed two types of quantitative dispersal networks that 1) accounted for frequency of interactions

(incidence networks) and 2) incorporated effectiveness of spore dispersal (disperser importance networks).

We address the following three questions: (1) Do rodent dietary specialists and generalists differ in their capacity to disperse fungal spores? We predicted that because fungal specialists consume more fungi, they will have higher richness and diversity of spores in their scat; (2) How do fluctuations in rodent abundance and their habitat affinity influence the relative importance of species in dispersal networks? We predicted that a species' relative importance would increase with their abundance and be highest in their preferred habitat (Schleuning et al. 2011). Furthermore, we hypothesized that abundance may offset dietary specialization, such that generalists can become among the most important dispersers when their abundance is high. (3) Does network structure vary among years and how does incorporating the effectiveness of dispersal interactions influence network structure? Because rodent population fluctuations are often synchronized among species (Stephens et al. 2017a), we predicted that during years of high rodent abundance, networks would be less specialized (Wells et al. 2014). Additionally, similar to pollination networks (e.g., Ballantyne et al. 2015), we predicted that incorporating the amount of spores dispersed by rodents would increase network specialization.

Methods

Study system and sample collection

We conducted our study in temperate forest at the Bartlett Experimental Forest, White Mountain National Forest, New Hampshire (44° 3′ 7.2″ N, 71° 17′ 25.1″ W) at elevations ranging from 250 to 450 m. The climate is humid continental, characterized by warm summers and cold winters. Sampling took place on 12 mark-recapture grids consisting of 64 trap stations and encompassing an area of 1.1 ha (8 × 8 station array with 15 m spacing). Average distance among grids was 1.23 km (range 0.28 - 2.61) and grids were stratified across mature hardwood

(*n* = 4), mixed (*n* = 4), and softwood (*n* = 4) forest. Hardwood grids were dominated by red maple (*Acer rubrum*) and American beech (*Fagus grandifolia*) with a lesser component of sugar maple (*A. saccharum*), yellow birch (*Betula alleghaniensis*), and white ash (*Fraxinus americana*). Softwood grids were dominated by eastern hemlock (*Tsuga canadensis*) and red spruce (*Picea rubens*) and mixed grids contained an assortment of species. Among forest types, truffle and mushroom biomass was circa 10 times greater in mixed and softwood forest than in hardwood forest (Stephens et al. 2017b).

We captured rodents using Sherman live traps (H. B. Sherman Co., Tallahassee, Florida) set within 1.5 m of each trap station and checked twice daily during a four consecutive day period in July and August in 2013 and in June, July, and August in 2014 – 2015. Traps were baited with bird seed and provisioned with polyester batting nesting material. All individuals were identified to species and marked with a uniquely numbered ear tag (model 1005-1; National Band and Tag Co., Newport, Kentucky). *Myodes gapperi* and *N. insignis* were also marked with a passive integrated transponder (pit tag- model HPT9; Biomark, Boise, Idaho) in 2014 and 2015 after high ear tag loss was observed in 2013. For dietary isotopic analyses, we collected approximately 1 to 4 mg of hair from an individual upon first capture and only took additional hair samples if molting occurred between trapping periods. To characterize rodent-mycorrhizal associations, we collected scat from Sherman traps upon first capture of an individual within a survey period (month). All traps with captures were washed and replaced with clean traps to ensure scat samples were not contaminated. The trapping protocol was approved by the University of New Hampshire Animal Care and Use Committee (protocols 120708 & 140304) and followed guidelines outlined by the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2016).

Our analyses were restricted to the five most common rodent species (*Myodes gapperi*, *Napaeozapus insignis*, *Tamias striatus*, *Peromyscus maniculatus*, and *P. leucopus*) that together represented > 98% of our total rodent individuals. *Myodes gapperi* is known to consume fungi as a major portion of its diet (Ure and Maser 1982, Orrock and Pagels 2002), whereas the other species have more generalized diets (DeGraaf and Yamasaki 2001). Shrews (*Sorex* spp. and *Blarina brevicauda*) were also common in our study area (Stephens et al. 2017a), but are primarily insectivorous and carry very low spore loads compared to rodents (Schickmann et al. 2012). We also restricted our analyses to data from July and August in order to standardize sampling across years and because the majority of mushroom and truffle taxa consumed by small mammals fruit during this time (Stephens et al. 2017b). Thus, our focus on rodent-fungal associations during July and August likely represent the vast majority of small mammal-fungal interactions that take place in this system.

Dietary classification

For each rodent species, we determined the proportion of the diet coming from fungi using stable isotopic analysis of hair and Bayesian mixing models implemented in the R package 'MixSIAR' (Stock and Semmens 2013). *MixSIAR* uses $\delta^{15}N$ and $\delta^{13}C$ values from both consumer tissues (i.e., hair) and food sources along with discrimination factors, elemental concentrations, and the uncertainties surrounding those values to calculate the relative proportion of food sources consumed. Details of isotopic analyses and mixing models can be found in the *stable isotope analysis* section of Appendix E.

Fungal taxa in rodent scat

For each grid within a year, we analyzed up to 10 scat samples per month from each rodent species. After collection, scat samples were frozen at -18 °C and prepared following methods outlined in Stephens et al. (2017b). Scat samples were freeze dried and ground to a powder. Approximately 20 mg of freeze-dried scat powder was weighed out to the nearest 0.1 mg, mixed with 5% KOH, and rinsed through a 125 mm screen (Gerson Elite paint strainers; Middleboro, MA, USA). After decanting the supernatant, the spore isolate was mixed with 95% ethanol and 100 μl spread onto a 22 x 22 mm portion of a glass slide. A drop of Visikol (chloral hydrate substitute- Phytosys LLC, New Brunswick, New Jersey, USA) and iodine were added to clear and stain the spores, respectively. After drying, the slide was sealed with Flo-Texx mounting medium (Lerner Laboratories, Pittsburgh, Pennsylvania, USA) and a cover slip. For each slide, we examined 25 non-overlapping fields of view at 400x magnification (combined area of 4.15 mm^2; 1% of slide) and counted the number of spores for each observed taxon. To detect taxa occurring at low abundance (i.e., not detected at 400x) we also scanned 121 mm^2 at 100x (25% of the slide). We used spore counts, the volume of spore isolate, and scat weight to calculate the total spore abundance per taxon (spore load) in 1 g of scat. Spores were identified to the lowest possible taxonomic unit (generally genus or species) using Castellano et al. (1989) and reference spores collected from sporocarps in the field (Castellano and Stephens 2017, Stephens et al. 2017b).

Spore dispersal effectiveness

Most studies investigating small mammal spore dispersal use richness of spores in scat as a measure of dispersal effectiveness, with higher richness indicating better dispersers (e.g., Nuske et al. 2017). However, in most systems, fungal taxa are not equally abundant (e.g., North

et al. 1997, Stephens et al. 2017b). For that reason, we calculated and compared both fungal spore richness and diversity (Shannon diversity index) among rodent species. Because spore abundances are inherently variable among fungal genera (Schickmann et al. 2012), for this analysis we used relativized spore abundance data (scaled across all scat samples within a fungal taxon). For richness and diversity comparisons we used mixed effects models implemented with 'lme' in the R package 'nlme' (Pinheiro et al. 2012). We included a random intercept of grid within year to account for the non-independence of samples from the same grid. Model fit was assessed by plotting residuals versus fitted values and by evidence of homogeneity of variances and normality of both the residuals and random effects (Zuur et al. 2009). Differences among rodent species was assessed using the R package 'emmeans' with *p*-values adjusted with Tukey's correction for multiple comparisons (Lenth 2018).

To determine if rodent species differed in dispersal effectiveness of individual fungal taxa, we compared the frequency of occurrence and spore loads from the 12 most common fungal taxa. Patterns were generally consistent among years and forest types and we pooled data to facilitate comparisons. Within each fungal taxon, we tested for differences in frequency of occurrence among the rodent species with a G-test goodness-of-fit. When significant, we used post hoc tests with Bonferroni correction for multiple comparisons. G-tests and post hoc tests were performed using 'G-test' and 'pariwise.G.test', respectively in the R-package 'RVAideMemoire' (Hervé 2016). For each fungal taxon, we also tested for differences in the abundance of spores carried among rodent species using the nonparametric Kruskal-Wallis test ('kruskal.test' in R). When significant, we performed Conover–Iman post hoc tests with Bonferroni correction for multiple comparisons using the R-package 'conover.test' (Dinno 2017).

Rodent abundance

Rodent population size may be influenced by extrinsic factors such as weather and food availability (Conrod and Reitsma 2015, Stephens et al. 2017a). During the fall of 2013, The White Mountain region experienced a mast fruiting event by American beech that created an abundant and high quality food source for rodents (Cleavitt and Fahey 2017). To determine if this influenced rodent populations, we used linear mixed effects models and Tukey post-hoc comparisons to test for differences among years and among forest types within a year. For a given year and grid, rodent abundance was calculated as the number of unique individuals captured during July and August. Our modeling approach followed the same process outlined for richness and diversity comparisons. For fixed effects we used year, forest type, and the interaction of year and forest type. We used a random intercept of grid within year to account for the repeated measures design.

Network construction

With the exception of a softwood grid in 2013, that only had one rodent species and could not be used to build a network, we constructed separate networks for each grid within a year (n = 35). Fungal sporocarps are sessile and only 0.4% of rodents (five individuals) moved between grids, supporting our assumption of independent communities. Sampling was adequate to detect most interactions within the dispersal network. Excluding one outlier that was removed from subsequent analyses (hardwood grid in 2013; 28% of pairwise interactions detected), an abundance-based richness estimator (Chao 1 – 'estimateR' in the R-package 'vegan'; Oksanen et al. 2014) indicated our sampling protocol detected 67% (range 48-83) of pairwise rodent-fungal interactions within grids. This is well within the range of other mutualistic network studies

(Costa et al. 2016). Moreover, our ability to detect interactions within a grid was not significantly correlated with the number of scat samples analyzed (n = 34, Pearson's r = 0.26, P = 0.14) nor was it significantly different among years (Appendix E, Table E1).

For the remaining grids within years (n = 34), we constructed two types of quantitative interaction networks: 1) incidence networks based on the frequency of rodent-fungal interactions (analogues to visitation networks in pollination studies, Ballantyne et al. 2015) and 2) disperser importance networks that combined the frequency of rodent-fungal interactions with average spore loads carried by each rodent species (analogues to the recently developed pollinator importance networks, Ballantyne et al. 2015). For incidence networks, we derived the total number of interactions between each rodent species and fungal taxa by multiplying grid specific rodent abundances by grid specific frequency interactions between rodent species and fungal taxa. Final matrices were scaled such that rodent species-fungal taxon interactions were the proportion of the total fungal taxon interactions from all rodent species; i.e., interaction bars for fungal taxa summed to one (Ballantyne et al. 2015). Scaling made it possible to make direct comparisons between incidence networks and disperser importance networks. To construct disperser importance networks, we multiplied the number of grid specific interactions between a rodent species and fungal taxa (used in incidence networks) by mean grid specific spore loads. Spore production varies greatly among sporocarps from different fungal taxa, which can influence the number of spores found in rodent scat (Schickmann et al. 2012). To control for this bias, final disperser importance matrices of rodent species-fungal taxon interactions were scaled as the proportion of the total spores dispersed per fungal taxon across all rodent species (i.e., interaction bars for fungal taxa summed to one).

Rodent importance and network structure

We analyzed incidence and disperser importance networks separately using the R package 'bipartite' (version 2.8; Dormann et al. 2008) and extracted network metrics. Additionally, using the 'plotweb' function within 'bipartite', we visualized changes in the structure of both network types among forest types and years. Matrices for plotweb visualizations were constructed from the average interactions (frequency or spore loads) within a forest type and year. To visualize overall changes in community level dispersal (i.e., total number of interactions and abundance of spores dispersed by the rodent community for a given fungal tax), we calculated the average number of rodent species-fungal taxon interactions and spores dispersed within a forest type and year.

To quantitatively characterize the overall importance of a rodent species within each network, we used species strength, which is the sum of dependencies of all fungal taxa for a given rodent species. This relative interaction weight within a network is a measure of the importance of a rodent species from the standpoint of the fungal community (Bascompte et al. 2006). When a rodent species was not present in a network, it was given a species strength of zero. To assess the relationship between rodent abundance and its importance in a network, we used Pearson's correlations between abundance and species strength for each rodent species and both network types. To compare the relative importance of a rodent species within a forest type and year, we performed analysis of variance (ANOVA) on species strength with grids as replicates. Incidence and disperser importance networks were analyzed separately. When the overall ANOVA was significant, Tukey's post hoc tests were used to determine pairwise differences between rodent species.

We used three community level metrics to test for changes in network structure among years and between the two network types. We used generality of fungal taxa, which is weighted to account for sample size (commonly referred to as vulnerability in the food web literature), to describe the mean effective number of fungal taxa that rodents disperse. To quantify specialization of networks, we used the standardized two-dimensional Shannon entropy index (H_2'), which is based on weighed links and is robust against sampling effort and differences in network size (Blüthgen et al. 2006). H_2' ranges from 0 (extreme generalization) to 1 (complete specialization). Lower values of network specialization indicate high niche breadth of rodents and fungi (fungal taxa are dispersed by a broad range of rodents), whereas high network specialization indicates narrow niche breadth (specialized fungal spore dispersal by rodent species). Interaction evenness of networks was used to describe the homogeneity in rodent-fungal interactions. Interaction evenness ranges from 0 to 1 with high values indicating that the number of interactions is relatively uniform among rodent species and fungal taxa.

For each community metric, we tested for differences among years and network type (incidence and dispersal importance) within a year using mixed effects models and post hoc comparisons with Tukey's correction. Procedures were the same as those used for rodent abundance analyses and included a random intercept of grid within year to account for the repeated measures design. Fixed effects included year, network type, and the interaction between year and network type. For each metric, forest types were combined within a year because they showed similar patterns in network structure.

Results

Diet and spore dispersal effectiveness

Isotopic mixing models indicated that *M. gapperi* was a fungal specialist with approximately 45% of its diet coming from fungi. The other four rodent species were dietary generalists with 20 - 23% of their diet coming from fungi (Fig. 4.1a).

We examined a total of 1,202 scat samples (2013-2015) from the rodent species (187 *M. gapperi*, 166 *N. insignis*, 173 *T. striatus*, 401 *P. maniculatus*, and 275 *P. leucopus*) and detected 34 fungal taxa, the vast majority of which are known to be mycorrhizal (91%) and truffles (76%; Appendix E, Table E2). All but 11 scat samples (<1%) contained fungal spores (1 *T. striatus*, 4 *P. maniculatus*, and 6 *P. leucopus*) and, among all samples, we observed a total of 4,163 rodent-fungal interactions (Appendix E, Table E2). Among rodent species, *Myodes gapperi* and *T. striatus* had the highest spore richness in their scat (Fig. 4.1b; Appendix E, Table E3) and *M. gapperi* had the highest spore diversity, followed by *T. striatus*, *Peromyscus* spp., and *N. insignis* (Fig. 4.1c; Appendix E, Table E3). Of the 12 most common fungal taxa, 11 showed significant differences in both occurrence rates (Appendix E, Table E2) and average spore loads (Appendix E, Table E4) carried by the rodent species. For occurrence proportions, *M. gapperi* and *T. striatus* were among the best dispersers for 7 and 8 of the 11 fungal taxa, respectively, whereas the other rodent species were among the best for only 3 to 5 taxa (Appendix E, Table E2). For spore loads, *M. gapperi* was among the best dispersers for 8 of the 11 fungal taxa, whereas the other rodent species were among the best for only 2 to 4 taxa (Appendix E, Table E4).

Rodent abundance

Over the three-year period, we captured 1245 unique rodent individuals during July and August (171 *M. gapperi*, 208 *N. insignis*, 123 *T. striatus*, 506 *P. maniculatus*, and 237 *P. leucopus*). We noted synchronous population fluctuations for *T. striatus* and *P. maniculatus*, both

being more abundant in 2014 (following masting of American beech) compared to either 2013 or 2015 (Fig. 4.2). Although this pattern was also seen for *P. leucopus* in mixed and softwood forest, it was only significant in softwood forest between 2013 and 2014. *Myodes gapperi* was the only species to show significant differences in abundance among forest types and was significantly more abundant in softwood forest than in hardwood forest during 2014 and 2015. Although *N. insignis* was often captured more in hardwood and mixed forest than softwood forest, there was considerable grid level variation and this pattern was not significant.

Rodent importance

The species strength (relative importance) of rodents in dispersal networks was significantly correlated with their abundance in both incidence (Pearson's r = 0.74 - 0.88) and disperser importance networks (Pearson's r = 0.59 – 0.87; Fig. 4.3). Compared to other rodent species, *P. maniculatus* had lower Pearson r values in both incidence disperser importance networks (Fig. 4.3). Although trends were similar for both incidence and disperser importance networks, the relative importance of *M. gapperi* and *T. striatus* tended to be higher in disperser importance networks than in incidence networks, whereas the opposite was true for the other rodent species, particularly *P. maniculatus* (Figs 4.3 and 4.4). *M. gapperi* consistently had the highest species strength in softwood forest where it was most abundant, and was similar in strength to other rodents in hardwood and mixed forest in 2013 and 2015, despite relatively low abundance (Figs 4.4 and 4.5). However, when the abundance of *T. striatus* and *P. maniculatus* increased in 2014, their species strength was similar to that of *M. gapperi* in softwood forest and was significantly higher in mixed and softwood forest (species strength from disperser importance networks shown in Fig 4.5; see Appendix E, Fig. E1for incidence networks). The

relative species strength of *N. insignis* and *P. leucopus* was also variable across years and forest types, but these species did not show consistent patterns.

Network structure

We detected significant differences in network metrics between network types and among years (Fig. 4.6). Fungal generality (measure of effective number of fungal taxa dispersed) was higher in incidence networks compared to disperser importance networks. Incidence networks showed moderate levels of network specialization (0.67 - 0.79) whereas disperser importance networks had high levels of network specialization (0.85-0.94), suggesting very specialized fungal spore dispersal by rodent species. Overall, both network types had high network evenness, although incidence networks had higher levels of evenness than disperser importance networks. For both network types, metrics were similar between 2013 and 2015; however, when *P. maniculatus* and *T. striatus* increased in abundance in 2014 following beech masting, fungal generality and network evenness increased and network specialization decreased relative to 2013 or 2015 (Figs 4.1 and 4.6). Additionally, the overall number of rodent-fungal interactions and relative abundance of spores dispersed was higher in 2014 compared to either 2013 or 2015 (Fig. 4.4).

Discussion

We found that rodent-mycorrhizal networks were highly dynamic among years and forest types. Overall, the fungal specialist, *Myodes gapperi* carried a relatively more diverse and abundant spore community compared to dietary generalists and was consistently the best fungal disperser in its preferred habitat. However, even after accounting for the better dispersal capacity of *M. gapperi*, generalists such as *T. striatus* and *P. maniculatus* were often the most important

dispersers when they reached high abundances. Our findings demonstrate that the interplay between abundance and habitat specificity strongly influenced a species importance within dispersal networks and that population fluctuations of dietary generalists can change network structure. Herein we discuss how rodent-mycorrhizal networks compare to other mutualistic network studies and how network dynamics may influence the ecosystem function of mycorrhizal dispersal.

Diet, abundance, and disperser importance

Nearly every rodent individual, irrespective of species, had at least one taxon of fungal spore in its scat, suggesting that mycophagy is common. Despite the ubiquity of mycophagy, we saw clear differences in the overall amount of fungi consumed and the overall effectiveness of spore dispersal by rodent species. Similar to other studies (e.g., Ure and Maser 1982, Orrock and Pagels 2002), we found that *M. gapperi* consumed fungi as a major portion of its diet and carried a rich and diverse mycorrhizal spore community in its scat. For most fungal taxa, *M. gapperi* carried far greater spore loads than the other rodent species. Although richness of spores in the scat of *T. striatus* was similar to that of *M. gapperi*, *T. striatus* carried relatively lower spore loads. *Tamias striatus* is the largest of the rodents in our community and because home range size is strongly correlated with body size (Lindstedt et al. 1986), it's likely that it forages over a broader area than the other rodent species. This may allow *T. striatus* to interact with a greater diversity of fungal sporocarps than other rodent generalists, despite consuming similar levels of fungi overall.

We found that rodent abundance strongly influenced rodent-mycorrhizal networks. This impact of abundance on species importance within a network has also been detected in other

mutualistic networks, both in model simulations and natural systems (e.g., Vázquez et al. 2007, Wells et al. 2014). Rodent species abundance was highly correlated with its relative importance within dispersal networks and was capable of offsetting dietary specialization (i.e., importance levels of generalist species were similar or higher than those of *M. gapperi*). However, this was most apparent only when *M. gapperi* populations were low. This suggests that habitat heterogeneity also plays an important role in structuring the relative importance of rodent species in dispersal networks. Similar to obligate bird frugivores that forage almost exclusively in habitats with high fruit diversity and abundance (Schleuning et al. 2011, Carlo and Morales 2016), *M. gapperi* was most abundant in mixed and softwood forest where truffle biomass was highest (Stephens et al. 2017b). In areas where food resources such as fruits and fungi are concentrated, dietary specialization may necessitate habitat specialization in order for species to meet food requirements. Thus, although dietary specialists provide consistent and important dispersal within their favored habitats, their overall impacts as spore dispersers across a heterogeneous landscape may be limited.

In habitats where dietary specialists are less common or absent, dietary generalists may fill the primary role as dispersal agents. For example, in Puerto Rico where birds disperse the majority of seeds, omnivores that are also habitat generalists provide critical dispersal into deforested areas as they actively forage across forested and open habitats whereas obligate frugivores only forage in forested areas (Carlo and Morales 2016). Similarly, the dietary generalists, *T. striatus* and the *Peromyscus* species, were often the primary dispersers of mycorrhizal fungi in hardwood and mixed forest. These rodent species are habitat generalists, occupying a variety of habitats from mature forest to open habitats throughout their geographic

range (Stephens and Anderson 2014). This habitat generalization may make them important dispersers of fungi into un-forested areas that lack existing mycorrhizal networks.

Dietary generalists further impacted network structure through their population fluctuations. Following masting of American beech trees, we observed synchronous abundance increases of generalists, particularly *T. striatus* and *P. maniculatus*. Coincident with these population increases we observed increases in the number of rodent-fungal interactions and, at the network level, there were effectively more fungal taxa dispersed and less specialization (i.e., more rodent species contributed to the dispersal of fungal taxa). The timing of these network changes likely plays an important role in forest ecosystem function. Specifically, trees such as American beech and eastern hemlock germinate in the spring and summer following a masting event (Marquis 1975, Wagner et al. 2010). During seedling establishment, inoculation by mycorrhizal fungi is critical to growth and survival (Terwilliger and Pastor 1999, Frank et al. 2009). The increased mycorrhizal dispersal provided by rodent generalists, particularly in hardwood and mixed forest, may provide important mycorrhizal inoculum to seedlings following germination.

Incidence vs disperser importance networks

Similar to pollinator networks, we found that rodent-mycorrhizal networks that accounted for interaction effectiveness (i.e., spore loads) had higher levels of network specialization and lower levels of network evenness and generality than networks based only on interaction frequency (incidence). However, unlike pollination communities that show relatively small differences between network types (Ballantyne et al. 2015, 2017), we found large differences, particularly for network specialization. This likely stems from the magnitude of the differences

in pollen grains vs. spore loads carried by pollinators and dispersers, respectively. For example, Ballantyne et al. (2015) found that the number of deposited pollen grains varied little among pollinators for a given plant species. Comparatively, for the majority of fungal taxa, we found that spore abundances differed by several orders of magnitude among rodent species (Appendix E, Table E4).

Spore abundance in scat is a product of both the amount of sporocarps consumed and time since ingestion, such that individuals that eat more sporocarps of a fungal taxa, more often, will have higher spore loads compared to species that only partially or occasionally eat sporocarps. Thus, similar to seed dispersal (Schupp et al. 2010), we believe that spore abundance data represent meaningful differences in dispersal potential and should be included in studies investigating mycophagy and mycorrhizal dispersal. Although both spore and seed abundance data are rarely considered in studies of dispersal networks (but see Ruggera et al. 2016), incorporating this information is likely a more realistic representation of dispersal effectiveness than interaction frequencies alone. Importantly, we found that incorporating the effectiveness of network interactions can change the interpretation of network structure. For example, we found that incidence networks were moderately specialized compared to the highly specialized disperser importance networks. Interestingly, both types of rodent-mycorrhizal networks had levels of specialization that are higher than what is commonly observed in seed dispersal networks ($H_2' = 0.30$), with incidence networks resembling pollinator networks ($H_2' = 0.60$) and disperser importance networks resembling ant-myrmecophyte networks ($H_2' = 0.80$; Blüthgen et al. 2007). This suggests that rodent species are fairly specialized in their selection of sporocarps and that they are ecologically complementary in their spore dispersal rather than redundant, particularly in years when rodent abundance is low.

Conclusions

The majority of studies investigating mammalian dispersal of mycorrhizal fungi have focused on fungal specialists including red-backed voles (*Myodes* spp.), northern flying squirrels (*Glaucomys sabrinus*), potoroos (*Potorous* spp.), and bettongs (*Bettongia* spp.; Maser et al. 2008). These fungal specialists are often considered to be the most important dispersers of mycorrhizal spores (e.g., Nuske et al. 2017). Our results suggest that fungal specialists are often just one of many species within the mammal community that interact with fungi and that to understand the relative importance of a species within the dispersal network it is important to consider abundance, habitat specificity, and habitat heterogeneity. Directly measuring the role of mycorrhizal-mediated dispersal by small mammal species is important for understanding how animals contribute to forest ecosystem function.

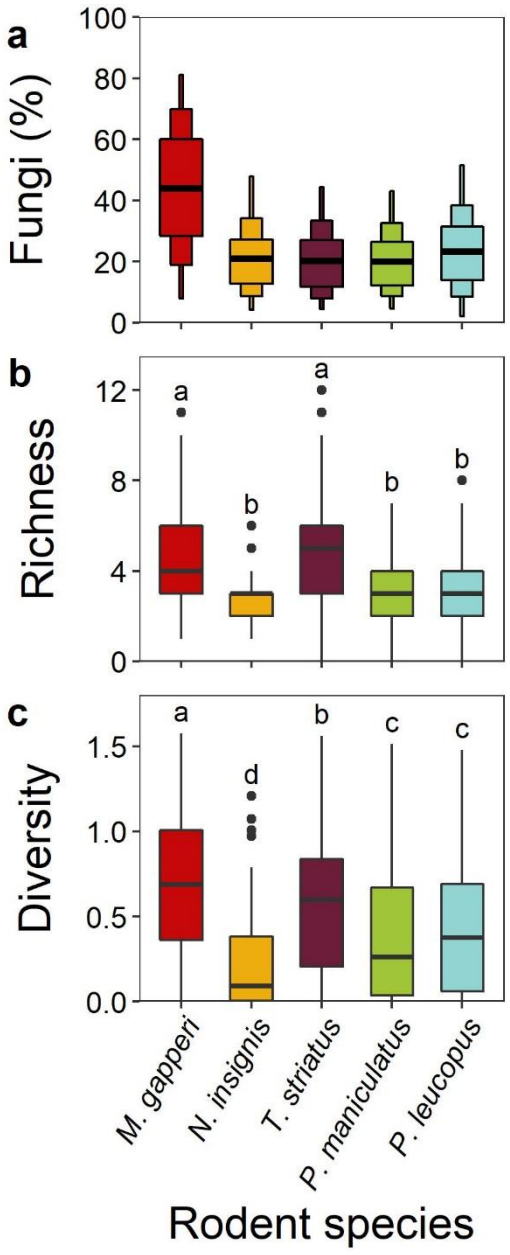


Figure 4.1. Consumption of fungi by rodent species. (a) Percent of fungi in the diet of rodent species as indicated by Bayesian mixing models, (b) taxon richness of fungal spores in scat, and (c) diversity of the fungal spore community in scat . Medians of fungal proportions are indicated by a thick horizontal bar and Bayesian credible intervals are denoted by box width (50% thick box; 75% intermediate box; and 95% thin box). Boxplots of richness are based on individual fungal taxa in scat and boxplots of diversity are the Shannon diversity index based on the abundance of spores after relativizing across all scat samples for each fungal taxa. Mixed effects models with Tukey's post tests were used to test for differences in richness and diversity among rodent species. Rodents with the same letters are not significantly different, whereas years with the same letters are significant different. Statistics for mixed effects models for spore richness and diversity can be found in Table E3 of Appendix E.

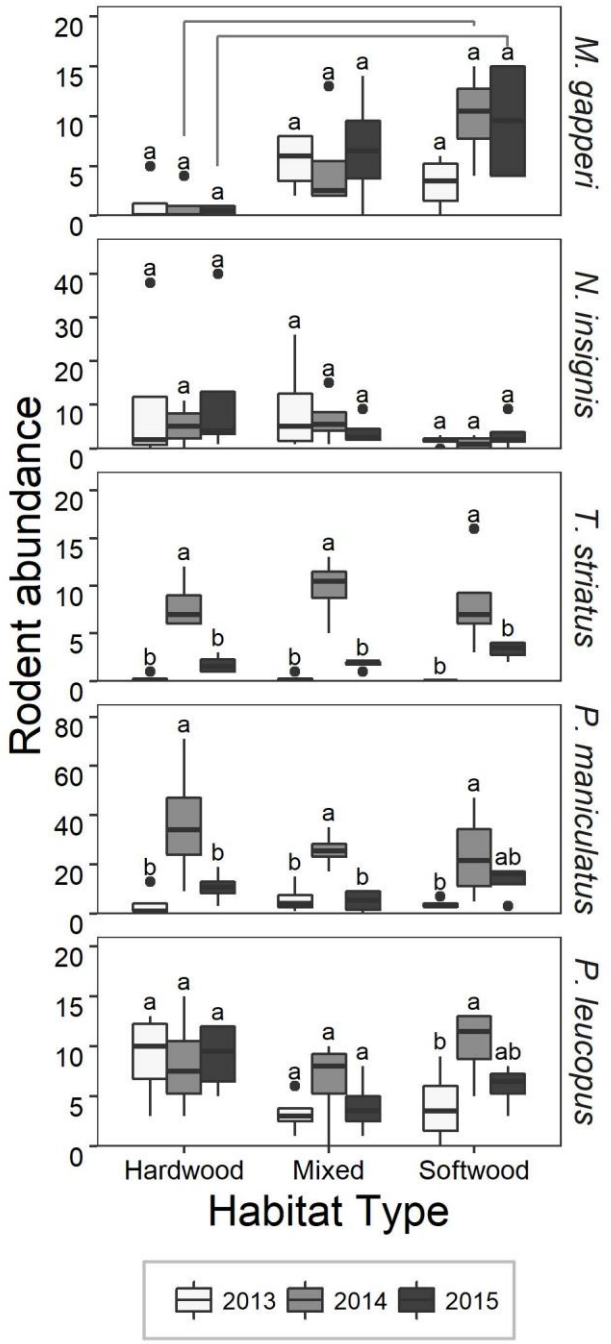


Figure 4.2. Boxplots of rodent abundance among forest types and years. For each rodent species, mixed effects models with Tukey's post tests were used to determine differences in abundance among years and forest types. Within a forest type, years with the same letters are not significantly different, whereas years with the same letters are significant different. For *Myodes gapperi*, lines above bars connect forest types with significantly different abundances within a year. No other rodent species showed significant differences among forest types. Statistics for mixed effects models can be found in Table E5 of Appendix E.

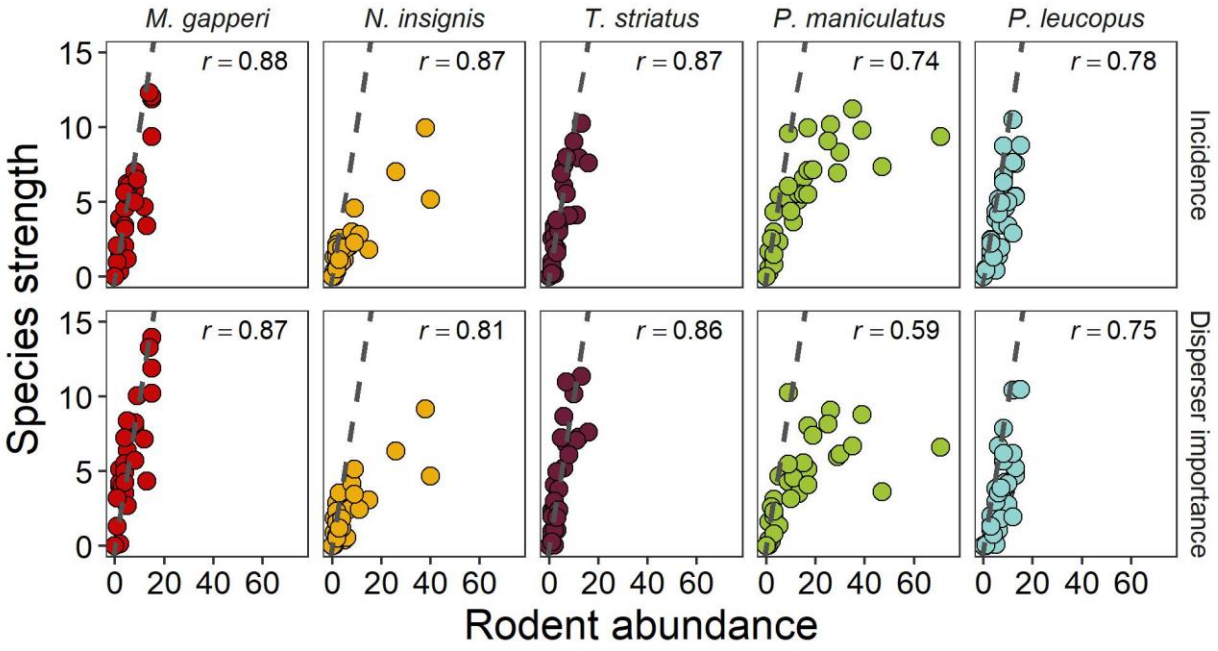


Figure 4.3. Relationship between abundance and species strength for rodents in incidence networks (top row) and disperser importance networks (bottom row). Pearson's correlations are shown in the upper right hand corner. All correlations were statistically significant ($P < 0.001$). Dashed line indicates a 1:1 relationship and is provided for reference.

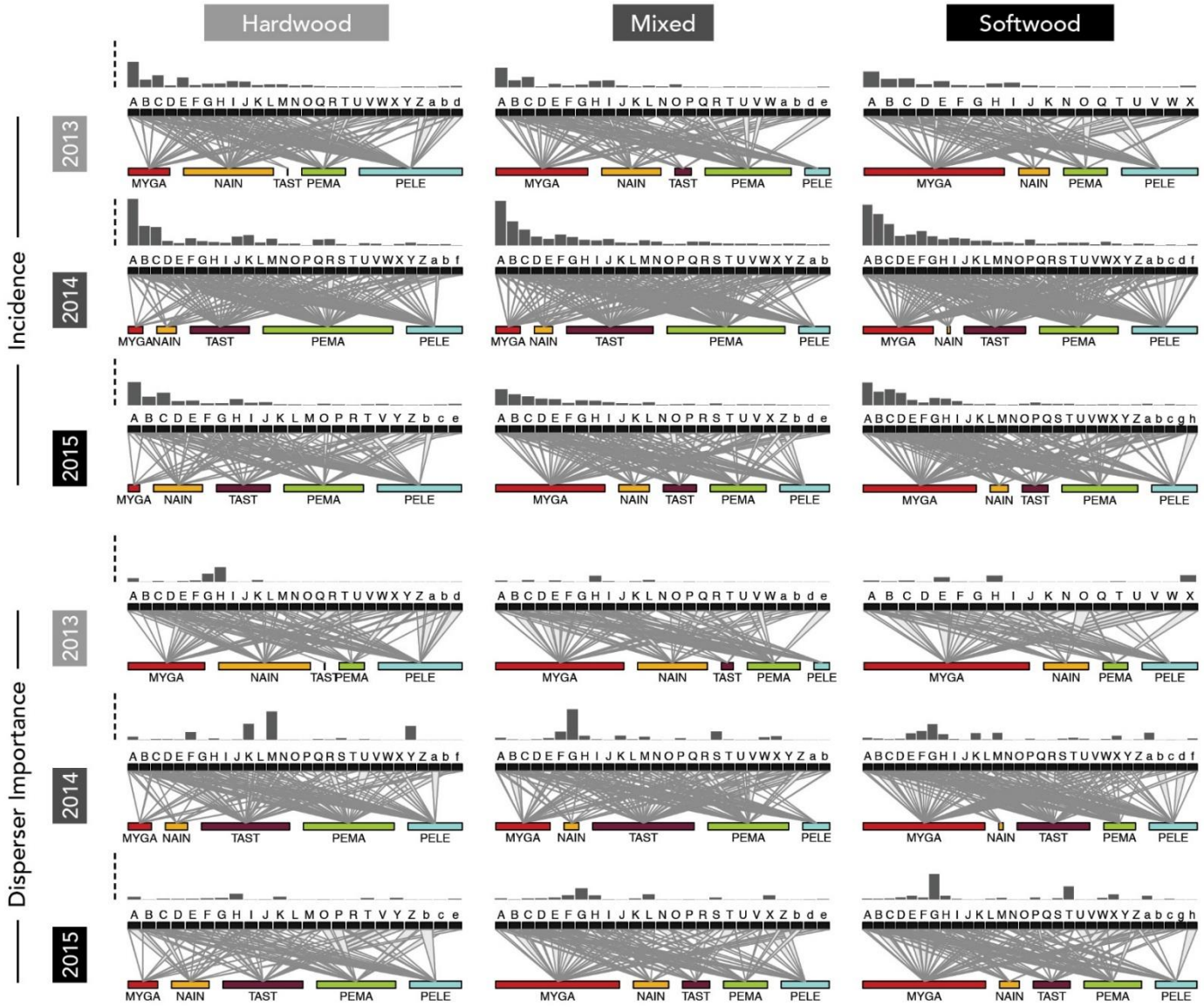

Hardwood
Mixed
Softwood
Incidence
Disperser Importance
2013
2014
2015
MYGA
NAIN
TAST
PEMA
PELE

Figure 4.4. Dynamics of incidence and disperser importance networks among forest types and years. Within a year, networks are based on the averages of four replicate trapping grids for each forest type, with the exception of hardwood and softwood forest types in 2013 that are based off of three replicates. Fungal taxa are indicated by letters and rodent species by four letter genus/species abbreviations (see below). For all networks, fungal taxa are standardized whereas the length of the bar for rodents represents their relative contribution to mycorrhizal dispersal. For a given fungal taxa, dark gray bars above letters denote average number of interactions with all rodent species in incidence networks and average number of spores carried by all rodent species in disperser importance networks. Dashed lines at far left side of bars denote 12 interaction and 50 million spores for incidence and disperser importance networks, respectively. Fungal taxa abbreviations: A (*Glomus*), B (*Elaphomyces verruculosus*), C (*Elaphomyces macrosporus*), D (*Elaphomyces bartlettii*), E (Russulaceae 1), F (Unknown 1), G (Boletaceae 1), H (Russulaceae 3), I (*Hydnotrya cubispora*), J (*Elaphomyces americanus*), K (*Octaviania*), L (*Cortinarius*), M (Unknown 2), N (Russulaceae 2), O (*Elaphomyces oreoides*), P (*Gauteria*), Q (*Endogone pisiformis*), R (*Hydnobolites*), S (*Rhizopogon*), T (Boletaceae 2), U (*Entoloma*), V (*Hydnotrya tulasnei*), W (*Hysterangium* spp. 3), X (*Leucogaster*), Y (*Melanogaster*), Z (*Tuber*), a (*Hysterangium* spp. 2), b (*Genea*), c (*Gymnomyces*), d (*Leucophleps*), e (*Hymenogaster*), f (*Hysterangium* spp. 1), g (*Chamonixia*), and h (*Elaphomyces remickii*). Rodent abbreviations: MYGA (*Myodes gapperi*), NAIN (*Napaeozapus insignis*), TAST (*Tamias striatus*), PEMA (*Peromyscus maniculatus*), and PELE (*Peromyscus leucopus*).

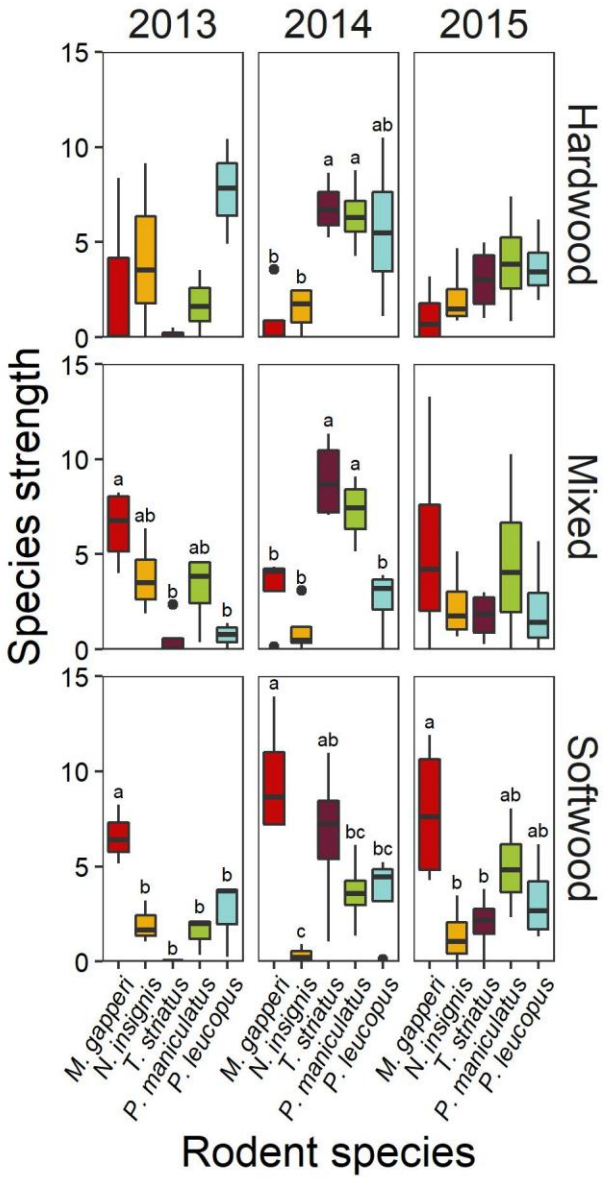


Figure 4.5. Boxplots indicating species strength of the five rodents in disperser importance networks. Within a given year and forest type, significant differences were determined with a ANOVA: 2013 Hardwood ($F_{4,10} = 2.23$; $P = 0.138$), 2014 Hardwood ($F_{4,15} = 6.21$; $P = 0.004$), 2015 Hardwood ($F_{4,15} = 6.21$; $P = 0.272$), 2013 Mixed ($F_{4,15} = 8.66$; $P < 0.001$), 2014 Mixed ($F_{4,15} = 13.43$; $P < 0.001$), 2015 Mixed ($F_{4,15} = 0.85$; $P = 0.518$), 2013 Softwood ($F_{4,10} = 10.33$; $P = 0.001$), 2014 Softwood ($F_{4,15} = 6.71$; $P = 0.003$), and 2014 Softwood ($F_{4,15} = 4.54$; $P = 0.013$). Rodents with the same letters are not significantly different, whereas rodents with different letters are significantly different.

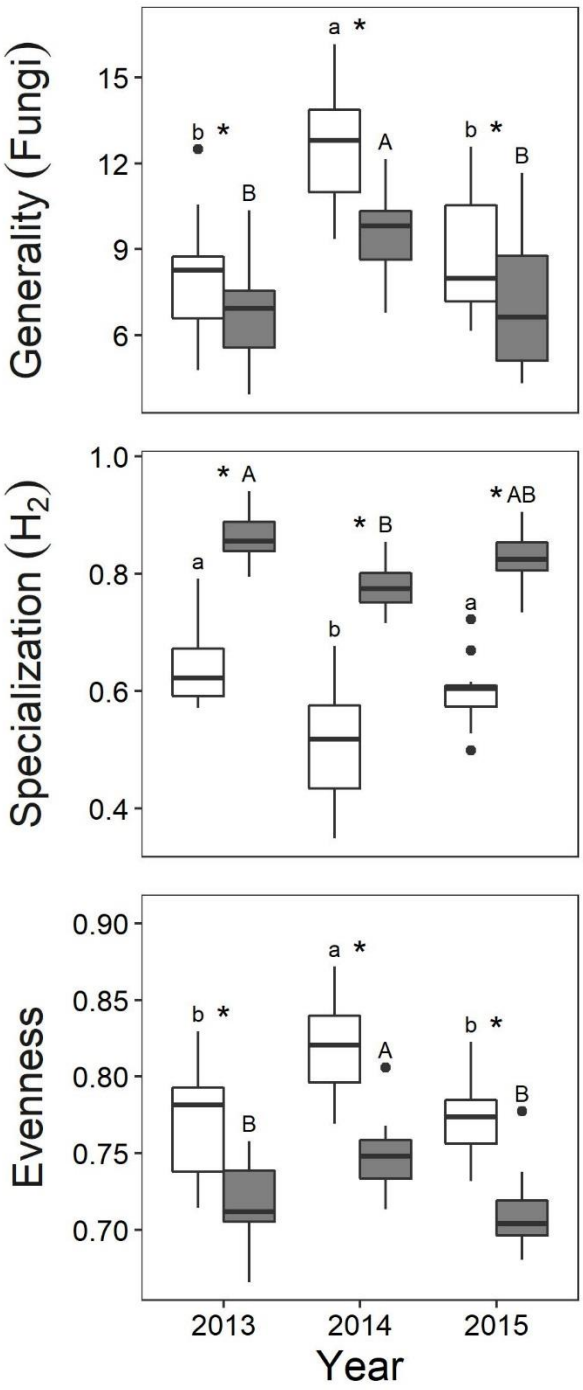


Figure 4.6. Boxplots of network-level metrics for incidence networks (white) and disperser importance networks (gray). For each metric, mixed effects models with Tukey's post hoc tests were used to test for differences among years and between network types. Within a network type, years with the same letters (lower case for incidence networks and upper case for disperser networks) are not significantly different, whereas years with different letters are significant different. Within a year, an asterisk denotes significant differences between network types. Statistics for mixed effects models can be found in Table E6 of Appendix E.

LITERATURE CITED

Abrams, P. 1983. The theory of limiting similarity. Annual Review of Ecology and Systematics 14:359–376.

Almeida, R. T., and N. C. Schenck. 1990. A Revision of the Genus *Sclerocystis* (Glomaceae, Glomales). Mycologia 82:703–714.

Amaranthus, M., J. M. Trappe, L. Bednar, and D. Arthur. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. Canadian Journal of Forest Research 24:2157–2165.

Andersen, D. C., and M. L. Folk. 1993. *Blarina brevicauda* and *Peromyscus leucopus* reduce overwinter survivorship of acorn weevils in an Indiana hardwood forest. Journal of Mammalogy 74:656–664.

Anderson, M. J., and D. C. I. Walsh. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecological Monographs 83:557–574.

Anderson, P., M. Brundrett, P. Grierson, and R. Robinson. 2010. Impact of severe forest dieback caused by *Phytophthora cinnamomi* on macrofungal diversity in the northern jarrah forest of Western Australia. Forest Ecology and Management 259:1033–1040.

Andersson, A. F., L. Riemann, and S. Bertilsson. 2010. Pyrosequencing reveals contrasting seasonal dynamics of taxa within Baltic Sea bacterioplankton communities. The ISME Journal 4:171–181.

de Assis Bomfim, J., P. R. Guimarães, C. A. Peres, G. Carvalho, and E. Cazetta. 2018. Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks. Ecography doi.org/10.

Ballantyne, G., K. C. R. Baldock, L. Rendell, and P. G. Willmer. 2017. Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. Scientific Reports 7:8389.

Ballantyne, G., K. C. R. Baldock, and P. G. Willmer. 2015. Constructing more informative plant-pollinator networks: visitation and pollen deposition networks in a heathland plant community. Proceedings of the Royal Society of London B: Biological Sciences 282:20151130.

Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312:431–433.

Belcher, C. F. 1980. Logging railroads of the White Mountains. Appalachian Mountain Club, Boston, MA.

Beug, M., A. E. Bessette, and A. R. Bessette. 2014. Ascomycete fungi of North America: a mushroom reference guide. University of Texas Press, Austin, Texas.

Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. Measuring specialization in species interaction networks. BMC Ecology 6:9.

Blüthgen, N., F. Menzel, T. Hovestadt, B. Fiala, and N. Blüthgen. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. Current Biology 17:341–346.

Bolnick, D. I., T. Ingram, W. E. Stutz, L. K. Snowberg, O. L. Lau, and J. S. Paull. 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proceedings of the Royal Society of London B: Biological Sciences 277:1789–1797.

Brooks, R. T., H. R. Smith, and W. M. Healy. 1998. Small-mammal abundance at three elevations on a mountain in central Vermont, USA: A sixteen-year record. Forest Ecology and Management 110:181–193.

Brown, B. L. 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. Ecology Letters 6:316–325.

Brown, L. N. 1963. Maturational molts and seasonal molts in *Peromyscus boylii*. American Midland Naturalist 70:466–469.

Campbell, J. L., and S. T. Gower. 2000. Detritus production and soil N transformations in old-growth eastern hemlock and sugar maple stands. Ecosystems 3:185–192.

Carey, A. B., W. Colgan III, J. M. Trappe, and R. Molina. 2002. Effects of forest management on truffle abundance and squirrel diets. Northwest Science 76:148–157.

Carlo, T. A., and J. M. Morales. 2016. Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. Ecology 97:1819–1831.

Castellano, M. A., T. M. James, Z. Maser, and C. Maser. 1989. Key to spores of the genera of hypogeous fungi of north temperate forests with special reference to animal mycophagy. Mad River Press, Inc., Eureka, California .

Castellano, M. A., and R. B. Stephens. 2017. *Elaphomyces* species (*Elaphomycetaceae, Eurotiales, Ascomycota*) from Bartlett Experimental Forest, New Hampshire, USA. IMA Fungus 8:49–63.

Cattadori, I. M., D. T. Haydon, and P. J. Hudson. 2005. Parasites and climate synchronize red grouse populations. Nature 433:737–741.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Claridge, A. W., S. C. Barry, S. J. Cork, and J. M. Trappe. 2000. Diversity and habitat relationships of hypogeous fungi. III. Factors influencing the occurrence and number of taxa. Biodiversity and conservation 9:175–199.

Clarkson, D. A., and L. S. Mills. 1994. Hypogeneous sporocarps in forest remnants and clearcuts in southwest Oregon. Northwest Science 68:259–265.

Cleavitt, N. L., and T. Fahey. 2017. Seed production of sugar maple and American beech in northern hardwood forests, New Hampshire, USA. Canadian Journal of Forest Research 47:985–990.

Clobert, J., M. Baguette, T. G. Benton, J. M. Bullock, and S. Ducatez. 2012. Dispersal ecology and evolution. Oxford University Press, Oxford, UK.

Cogbill, C. V. 2000. Vegetation of the presettlement forests of northern New England and New York. Rhodora 102:250–276.

Colgan III, W., A. B. Carey, J. M. Trappe, R. Molina, and D. Thysell. 1999. Diversity and productivity of hypogeous fungal sporocarps in a variably thinned Douglas-fir forest. Canadian Journal of Forest Research 29:1259–1268.

Colgan, W., and A. W. Claridge. 2002. Mycorrhizal effectiveness of *Rhizopogon* spores recovered from faecal pellets of small forest-dwelling mammals. Mycological Research 106:314–320.

Collins, H. H. 1923. Studies of the pelage phases and of the nature of color variations in mice of the genus *Peromyscus*. Journal of Experimental Zoology 38:45–107.

Conrod, C. A., and L. Reitsma. 2015. Demographic responses of myomorph rodents to mast production in a beech-and birch-dominated northern hardwood forest. Northeastern Naturalist 22:746–761.

Cork, S. J., and G. J. Kenagy. 1989a. Nutritional value of hypogeous fungus for a forest-dwelling ground squirrel. Ecology 70:577–586.

Cork, S. J., and G. J. Kenagy. 1989b. Rates of gut passage and retention of hypogeous fungal spores in two forest-dwelling rodents. Journal of Mammalogy 70:512–519.

Correa, S. B., and K. O. Winemiller. 2014. Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forest. Ecology 95:210–224.

Costa, J. M., L. P. da Silva, J. A. Ramos, and R. H. Heleno. 2016. Sampling completeness in seed dispersal networks: When enough is enough. Basic and Applied Ecology 17:155–164.

Costello, C. A., M. Yamasaki, P. J. Pekins, W. B. Leak, and C. D. Neefus. 2000. Songbird response to group selection harvests and clearcuts in a New Hampshire northern hardwood forest. Forest Ecology and Management 127:41–54.

Cramer, M. J. 2014. Seeds of doubt: feeding preferences of white-footed deer mice (*Peromyscus leucopus noveboracensis*) and woodland deer mice (*Peromyscus maniculatus gracilis*) on maple (genus *Acer*) seeds. Canadian Journal of Zoology 92:771–776.

Crump, B. C., and J. E. Hobbie. 2005. Synchrony and seasonality in bacterioplankton communities of two temperate rivers. Limnology and Oceanography 50:1718–1729.

Crump, B. C., B. J. Peterson, P. A. Raymond, R. M. Amon, A. Rinehart, J. W. McClelland, and R. M. Holmes. 2009. Circumpolar synchrony in big river bacterioplankton. Proceedings of the National Academy of Sciences of USA 106:21208–21212.

Dail, D., and L. Madsen. 2011. Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67:577–587.

Dalerum, F., and A. Angerbjörn. 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144:647–658.

Danks, M. A. 2012. Gut-retention time in mycophagous mammals: a review and a study of truffle-like fungal spore retention in the swamp wallaby. Fungal Ecology 5:200–210.

Danks, M., T. Lebel, K. Vernes, and N. Andrew. 2013. Truffle-like fungi sporocarps in a eucalypt-dominated landscape: patterns in diversity and community structure. Fungal Diversity 58:143–157.

Daubenmire, R. F. 1930. The relation of certain ecological factors to the inhibition of forest floor herbs under hemlock. Vol. 1. Butler University Botanical Studies, 61–76.

Davidson, D. L., and D. W. Morris. 2001. Density-dependent foraging effort of deer mice (*Peromyscus maniculatus*). Functional Ecology 15:575–583.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

DeGraaf, R. M., D. P. Snyder, and B. J. Hill. 1991. Small mammal habitat associations in poletimber and sawtimber stands of four forest cover types. Forest Ecology and Management 46:227–242.

DeGraaf, R. M., and M. Yamasaki. 2001. New England wildlife: habitat, natural history, and distribution. University Presss of New England, Hanover, New Hampshire, USA.

Dingman, S. L. 1981. Elevation: a major influence on the hydrology of New Hampshire and Vermont, USA. Hydrological Sciences Journal 26:399–413.

Dinno, A. 2017. conover.test: Conover-Iman test of multiple comparisons using rank sums. R package version 1.1.5. https://CRAN.R-project.org/package=conover.test.

Donaldson, R., and M. Stoddart. 1994. Detection of hypogeous fungi by Tasmanian bettong (*Bettongia gaimardi*: Marsupialia; Macropodoidea). Journal of Chemical Ecology 20:1201–1207.

Donatti, C. I., P. R. Guimarães, M. Galetti, M. A. Pizo, F. Marquitti, and R. Dirzo. 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. Ecology Letters 14:773–781.

Dooley Jr., J. L., and R. D. Dueser. 1990. An experimental examination of nest-site segregation by two *Peromyscus* species. Ecology 71:788–796.

Dormann, C. F., B. Gruber, and J. Fründ. 2008. Introducing the bipartite package: analysing

ecological networks. R News 8:8–11.

Dubay, S. A., G. D. Hayward, and C. Martinez del Rio. 2008. Nutritional value and diet preference of arboreal lichens and hypogeous fungi for small mammals in the Rocky Mountains. Canadian Journal of Zoology 86:851–862.

Egoscue, H. J., J. G. Bittmenn, and J. A. Petrovich. 1970. Some fecundity and longevity records for captive small mammals. Journal of Mammalogy 51:622–623.

Elias, S. P., J. W. Witham, and M. L. Hunter Jr. 2004. *Peromyscus leucopus* abundance and acorn mast: population fluctuation patterns over 20 years. Journal of Mammalogy 85:743–747.

Escribano-Avila, G., M. Calviño-Cancela, B. Pías, E. Virgos, F. Valladares, and A. Escudero. 2014. Diverse guilds provide complementary dispersal services in a woodland expansion process after land abandonment. Journal of Applied Ecology 51:1701–1711.

Escribano-Avila, G., C. Lara-Romero, R. Heleno, and A. Traveset. 2018. Tropical seed dispersal networks: emerging patterns, biases, and keystone species traits. Pages 93–110 *in* W. Dáttilo and V. Rico-Gray, editors. Ecological networks in the tropics: an integrative overview of species interactions from some of the most species-rich habitats on earth. Springer International Publishing, Cham.

Etienne, R. S., and H. Olff. 2004. How dispersal limitation shapes species-body size distributions in local communities. American Naturalist 163:69–83.

Falls, J. B., A. E. Falls, and J. M. Fryxell. 2007. Fluctuations of deer mice in Ontario in relation to seed crops. Ecological Monographs 77:19–32.

Filzmoser, P., and M. Gschwandtner. 2017. mvoutlier: multivariate outlier detection based on robust methods. R package version 2.0.8:https://cran.r-project.org/web/packages/mvoutlier/.

Fletcher, Q. E., S. Boutin, J. E. Lane, J. M. LaMontagne, A. G. McAdam, C. J. Krebs, and M. M. Humphries. 2010. The functional response of a hoarding seed predator to mast seeding. Ecology 91:2673–2683.

Fogel, R. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas fir stand. Canadian Journal of Botany 54:1152–1162.

Foster, D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire, USA. Journal of Ecology 76:105–134.

Fox, J. W., G. Legault, D. A. Vasseur, and J. A. Einarson. 2013. Nonlinear effect of dispersal rate on spatial synchrony of predator-prey cycles. PLoS ONE 8:e79527.

Frank, J. L., S. Anglin, E. M. Carrington, D. S. Taylor, B. Viratos, and D. Southworth. 2009. Rodent dispersal of fungal spores promotes seedling establishment away from mycorrhizal networks on *Quercus garryana*. Botany 87:821–829.

Fraser, E. E., F. J. Longstaffe, and M. B. Fenton. 2013. Moulting matters: the importance of understanding moulting cycles in bats when using fur for endogenous marker analysis. Canadian Journal of Zoology 91:533–544.

Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1995. Species compensation and complementarity in ecosystem function. Pages 224–239 *in* C. G. Jones and J. H. Lawton, editors. Linking Species and Ecosystems. Chapman and Hall, New York, USA.

Garnas, J. R., M. P. Ayres, A. M. Liebhold, and C. Evans. 2011. Subcontinental impacts of an invasive tree disease on forest structure and dynamics. Journal of Ecology 99:532–541.

Gervais, J. A., and N. T. Wheelwright. 1994. Winter fruit removal in four plant species in Maine. Maine Naturalist 2:15–24.

Gesch, D., M. Oimoen, S. Greenlee, C. Nelson, M. Steuck, and D. Tyler. 2002. The national elevation dataset. Photogrammetric Engineering and Remote Sensing 68:5–11.

Gomez, D. M., R. G. Anthony, and J. P. Hayes. 2005. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. Journal of Wildlife Management 69:1670–1682.

Gottschang, J. L. 1956. Juvenile molt in *Peromyscus leucopus noveboracensis*. Journal of Mammalogy 37:516–520.

Gouhier, T. C., F. Guichard, and A. Gonzalez. 2010. Synchrony and Stability of Food Webs in Metacommunities. The American Naturalist 175:E16–E34.

Grenfell, B. T., O. N. Bjørnstad, and J. Kappey. 2001. Travelling waves and spatial hierarchies in measles epidemics. Nature 414:716–723.

Grodziński, W., and K. Sawicka-Kapusta. 1970. Energy values of tree-seeds eaten by small mammals. Oikos 21:52–58.

Hamilton Jr., W. J. 1941. The food of small forest mammals in eastern United States. Journal of Mammalogy 22:250–263.

Hansen, B. B., V. Grøtan, R. Aanes, B.-E. Sæther, A. Stien, E. Fuglei, R. A. Ims, N. G. Yoccoz, and Å. Ø. Pedersen. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. Science 339:313–315.

Hanski, I., and E. Korpimaki. 1995. Microtine rodent dynamics in northern Europe: parameterized models for the predator-prey interaction. Ecology 76:840–850.

Havill, N. P., M. E. Montgomery, G. Yu, S. Shiyake, and A. Caccone. 2006. Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. Annals of the Entomological Society of America 99:195–203.

Haygreen, J. G., and J. L. Bower. 1989. Forest products and wood science, an introduction. second ed. Iowa State University Press, Ames, Iowa.

Hervé, M. 2016. RVAideMemoire: Diverse Basic Statistical and Graphical Functions. R package version 0.9-62:https://CRAN.R-project.org/package=RVAideMemoire.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65–70.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346–363.

Houlahan, J. E., D. J. Currie, K. Cottenie, G. S. Cumming, S. K. M. Ernest, C. S. Findlay, S. D. Fuhlendorf, U. Gaedke, P. Legendre, and J. J. Magnuson. 2007. Compensatory dynamics are rare in natural ecological communities. Proceedings of the National Academy of Sciences 104:3273–3277.

Houle, G. 1994. Spatiotemporal patterns in the components of regeneration of four sympatric tree species--*Acer rubrum*, *A. saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*. Journal of Ecology 82:39–53.

Hughes, J. W., and T. J. Fahey. 1988. Seed dispersal and colonization in a disturbed northern hardwood forest. Bulletin of the Torrey Botanical Club 115:89–99.

Huitu, O., J. Laaksonen, T. Klemola, and E. Korpimäki. 2008. Spatial dynamics of *Microtus* vole populations in continuous and fragmented agricultural landscapes. Oecologia 155:53–61.

Hunt, G. A., and J. M. Trappe. 1987. Seasonal hypogeous sporocarp production in a western Oregon Douglas-fir stand. Canadian Journal of Botany 65:438–445.

Ims, R. A., and H. P. Andreassen. 2000. Spatial synchronization of vole population dynamics by predatory birds. Nature 408:194–196.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595–602.

Jensen, T. S. 1985. Seed-seed predator interactions of European beech, *Fagus silvatica* and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. Oikos 44:149–156.

Jensen, T. S., and O. F. Nielsen. 1986. Rodents as seed dispersers in a heath—oak wood succession. Oecologia 70:214–221.

Johnson, C. 1994a. Fruiting of hypogeous fungi in dry sclerophyll forest in Tasmania, Australia: seasonal variation and annual production. Mycological Research 98:1173–1182.

Johnson, C. N. 1994b. Mycophagy and spore dispersal by a rat-kangaroo: consumption of ectomycorrhizal taxa in relation to their abundance. Functional Ecology 8:464–468.

Kelt, D. A., D. H. Van Vuren, M. L. Johnson, J. A. Wilson, R. J. Innes, B. R. Jesmer, K. P. Ingram, J. R. Smith, S. W. Bigelow, and R. D. Burnett. 2013. Small mammals exhibit limited spatiotemporal structure in Sierra Nevada forests. Journal of Mammalogy 94:1197–1213.

Kent, A. D., A. C. Yannarell, J. A. Rusak, E. W. Triplett, and K. D. Mcmahon. 2007. Synchrony in aquatic microbial community dynamics. The ISME Journal 1:38–47.

Kéry, M. 2010. Introduction to WinBUGS for ecologists- a Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press, Burlington, Massachusetts, USA.

King, D. I., M. Yamasaki, R. M. DeGraaf, and C. A. Costello. 2011. Three decades of avian research on the Bartlett Experimental Forest, New Hampshire, USA. Forest Ecology and Management 262:3–11.

Koenig, W. D., and J. M. H. Knops. 1998. Scale of mast-seeding and tree-ring growth. Nature 396:225–226.

Korpimäki, E., K. Norrdahl, O. Huitu, and T. Klemola. 2005. Predator–induced synchrony in population oscillations of coexisting small mammal species. Proceedings of the Royal Society of London B: Biological Sciences 272:193–202.

Krebs, C. J., A. J. Kenney, S. Gilbert, K. Danell, A. Angerbjörn, S. Erlinge, R. G. Bromley, C. Shank, and S. Carriere. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. Canadian Journal of Zoology 80:1323–1333.

Krebs, C. J., and J. H. Myers. 1974. Population cycles in small mammals. Advances in Ecological Research 8:267–399.

Leak, W. B. 1974. Some effects of forest preservation. US Forest Service Research Note NE-186, Northeastern Forest Experiment Station, Uppper Darby, Pennsylvania, USA.

Leak, W. B. 1991. Secondary forest succession in New Hampshire, USA. Forest Ecology and Management 43:69–86.

Leak, W. B., and R. E. Graber. 1974. Forest vegetation related to elevation in the White Mountains of New Hampshire. US Department of Agriculture Forest Service, Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA.

Leak, W. B., and R. E. Graber. 1993. Six-year beechnut production in New Hampshire. Page Research Paper NE-677. USDA Forest Service, Northeastern Forest Experiment Station, Radnor, PA.

Leak, W. B., and M. Yamasaki. 2010. Seventy-year record of changes in the composition of overstory species by elevation on the Bartlett Experimental Forest. US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, USA.

Lenth, R. V. 2018. Emmeans: Estimated marginal means, aka least-squares means. R package:Package Version 1.1.2.

Liebhold, A., W. D. Koenig, and O. N. Bjornstad. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology and Systematics 35:467–490.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in

mammals. Ecology 67:413–418.

Linzey, D. W., and A. V Linzey. 1973. Notes on food of small mammals from Great Smoky Mountains National Park, Tennessee-North Carolina. Journal of Elisha Mitchell Scientific Society 89:6–14.

Loeb, S. C., F. H. Tainter, and E. Cázares. 2000. Habitat associations of hypogeous fungi in the Southern Appalachians: implications for the endangered northern flying squirrel (*Glaycomys sabrinus coloratus*). American Midland Naturalist 144:286–296.

Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. American Naturalist 172:E48–E66.

Lovejoy, D. A. 1975. The effect of logging on small mammal populations in New England northern hardwoods. Occasional Papers Biology Science Series, Univiversity of Connecticut 2:269–291.

Luoma, D. L., J. L. Eberhart, R. Molina, and M. P. Amaranthus. 2004. Response of ectomycorrhizal fungus sporocarp production to varying levels and patterns of green-tree retention. Forest Ecology and Management 202:337–354.

Luoma, D. L., and R. E. Frenkel. 1991. Fruiting of hypogeous fungi in Oregon Douglas-fir forests: seasonal and habitat variation. Mycologia 83:335–353.

Luoma, D. L., R. E. Frenkel, and J. M. Trappe. 1991. Fruiting of hypogeous fungi in Oregon Douglas-Fir forests: seasonal and habitat variation. Mycologia 83:335–353.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. The American Naturalist 100:603–609.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101:377–385.

Madsen, T., and R. Shine. 1999. Rainfall and rats: climatically driven dynamics of a tropical rodent population. Australian Journal of Ecology 24:80–89.

Marquis, D. A. 1975. Seed storage and germination under northern hardwood forests. Canadian Journal of Forest Research 5:478–484.

Maser, C., A. W. Claridge, and J. M. Trappe. 2008. Trees, truffles, and beasts: how forests function. Rutgers University Press.

Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799–809.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403–416.

Mauseth, J. D. 1988. Plant anatomy. Benjamin/Cummings Publishing Co., Menlo Park, California.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, USA. http://www.umass.edu/landeco/research/fragstats/fragstats.html.

Merritt, J. F., M. Lima, and F. Bozinovic. 2001. Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. Oikos 94:505–514.

Meyer, M. D., and M. P. North. 2005. Truffle abundance in riparian and upland mixed-conifer forest of California's southern Sierra Nevada. Canadian Journal of Botany 83:1015–1020.

Michel, N. L., A. C. Smith, R. G. Clark, C. A. Morrissey, and K. A. Hobson. 2015. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography 38:1–13.

Micheli, F., K. L. Cottingham, J. Bascompte, O. N. Bjørnstad, G. L. Eckert, J. M. Fischer, T. H. Keitt, B. E. Kendall, J. L. Klug, and J. A. Rusak. 1999. The dual nature of community variability. Oikos 85:161–169.

Moore, J. W., and B. X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11:470–480.

Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. Australian Journal of Zoology 1:291–298.

Mouquet, N., and M. Loreau. 2003. Community patterns in source-sink metacommunities. The American Naturalist 162:544–557.

Myers, J. H. 1998. Synchrony in outbreaks of forest lepidoptera: a possible example of the Moran effect. Ecology 79:1111–1117.

Myster, R. W., and S. T. A. Pickett. 1993. Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. Oikos 66:381–388.

Nathan, R., F. M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot, and A. Tsoar. 2008. Mechanisms of long-distance seed dispersal. Trends in Ecology & Evolution 23:638–647.

North, M. 2012. Managing Sierra Nevada forests. P. 184 in United States Department of Agriculture Forest Service, Albany, California. Technical Report PSW-GTR-23:1–184.

North, M., and J. Greenberg. 1998. Stand conditions associated with truffle abundance in western hemlock/Douglas-fir forests. Forest Ecology and Management 112:55–66.

North, M., P. Stine, K. O'Hara, W. Zielinski, S. Stephens, and others. 2009. An ecosystem management strategy for Sierran mixed-conifer forests. United States Department of Agriculture Forest Service, Albany, California. Technical Report PSW-GTR-2:1–49.

North, M., J. Trappe, and J. Franklin. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. Ecology 78:1543–1554.

Nuske, S. J., K. Vernes, T. W. May, A. W. Claridge, B. C. Congdon, A. Krockenberger, and S.

E. Abell. 2017. Redundancy among mammalian fungal dispersers and the importance of declining specialists. Fungal Ecology 27:1–13.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2014. Vegan:community ecology package.

Orrock, J. L., and J. F. Pagels. 2002. Fungus consumption by the southern red-backed vole (*Clethrionomys gapperi*) in the southern Appalachians. American Midland Naturalist 147:413–418.

Orwig, D. A., and D. R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. Journal of the Torrey Botanical Society 125:60.

Orwig, D. A., D. R. Foster, and D. L. Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. Journal of Biogeography 29:1475–1487.

Ostfeld, R. S. 1997. The ecology of Lyme-disease risk: complex interactions between seemingly unconnected phenomena determine risk of exposure to this expanding disease. American Scientist 85:338–346.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology & Evolution 15:232–237.

Paradis, A., J. Elkinton, K. Hayhoe, and J. Buonaccorsi. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. Mitigation and Adaptation Strategies for Global Change 13:541–554.

Perry, D. A., M. P. Amaranthus, J. G. Borchers, S. L. Borchers, and R. E. Brainerd. 1989. Bootstrapping in Ecosystems. BioScience 39:230–237.

Perry, G., and E. R. Pianka. 1997. Animal foraging: past, present and future. Trends in Ecology & Evolution 12:360–364.

Pigot, A. L., T. Bregman, C. Sheard, B. Daly, R. S. Etienne, and J. A. Tobias. 2016. Quantifying species contributions to ecosystem processes: a global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks. Proc. R. Soc. B 283:20161597.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team. 2012. nlme: linear and nonlinear mixed effects models. R package, version 3.1–105. http://cran.r-project.org/web/packages/nlme/index.html.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-plus. Springer-Verlag, New York, New York.

Piovesan, G., and J. M. Adams. 2001. Masting behaviour in beech: linking reproduction and climatic variation. Canadian Journal of Botany 79:1039–1047.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs

sampling. Page *in* K Hornik, F Leisch, and A Zeileis, editors. Proceedings of the 3rd International Workshop on Distributed Statistical Computing . Vienna, Austria.

Plummer, M. 2013. Package "rjags." The comprehensive R archive network <http://cran.r-project.org/>.

Portnoy, J. W., and W. E. Dodge. 1979. Red-shouldered hawk nesting ecology and behavior. The Wilson Bulletin 91:104–117.

Prugh, L. R., and C. D. Golden. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. Journal of Animal Ecology 83:504–514.

Pyare, S., and W. S. Longland. 2001. Mechanisms of truffle detection by northern flying squirrels. Canadian Journal of Zoology 79:1007–1015.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. version 3.3.1. http://www.R-project.org.

Reed, A. W., G. A. Kaufman, and D. W. Kaufman. 2006. Species richness-productivity relationship for small mammals along a desert-grassland continuum: differential responses of functional groups. Journal of Mammalogy 87:777–783.

Reid, R. E. B., E. N. Greenwald, Y. Wang, and C. C. Wilmers. 2013. Dietary niche partitioning by sympatric *Peromyscus boylii* and *P. californicus* in a mixed evergreen forest. Journal of Mammalogy 94:1248–1257.

Reiners, W. A., and G. E. Lang. 1979. Vegetational patterns and processes in the balsam fir zone, White Mountains New Hampshire. Ecology 60:403–417.

Richardson, A. D., J. P. Jenkins, B. H. Braswell, D. Y. Hollinger, S. V. Ollinger, and M.-L. L. Smith. 2007. Use of digital webcam images to track spring green-up in a deciduous broadleaf forest. Oecologia 152:323–334.

Rowe, R. J., R. C. Terry, and E. A. Rickart. 2011. Environmental change and declining resource availability for small-mammal communities in the Great Basin. Ecology 92:1366–1375.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Ruggera, R. A., P. G. Blendinger, M. D. Gomez, and C. Marshak. 2016. Linking structure and functionality in mutualistic networks: do core frugivores disperse more seeds than peripheral species? Oikos 125:541–555.

Schaller, M., J. D. Blum, S. P. Hamburg, and M. A. Vadeboncoeur. 2010. Spatial variability of long-term chemical weathering rates in the White Mountains, New Hampshire, USA. Geoderma 154:294–301.

Schickmann, S., A. Urban, K. Kräutler, U. Nopp-Mayr, and K. Hackländer. 2012. The

interrelationship of mycophagous small mammals and ectomycorrhizal fungi in primeval, disturbed and managed Central European mountainous forests. Oecologia 170:395–409.

Schleuning, M., N. Blüthgen, M. Flörchinger, J. Braun, H. M. Schaefer, and K. Böhning-Gaese. 2011. Specialization and interaction strength in a tropical plant--frugivore network differ among forest strata. Ecology 92:26–36.

Schnurr, J. L., R. S. Ostfeld, and C. D. Canham. 2002. Direct and indirect effects of masting on rodent populations and tree seed survival. Oikos 96:402–410.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Schoener, T. W. 1982. The controversy over interspecific competition: despite spirited criticism, competition continues to occupy a major domain in ecological thought. American Scientist 70:586–595.

Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188:333–353.

Sebastián-González, E. 2017. Drivers of species role in avian seed-dispersal mutualistic networks. Journal of Animal Ecology 86:878–887.

Selva, N., K. A. Hobson, A. Cortés-Avizanda, A. Zalewski, and J. A. Donázar. 2012. Mast pulses shape trophic interactions between fluctuating rodent populations in a primeval forest. PLoS ONE 7:e51267.

Shaner, P. J., M. Bowers, and S. Macko. 2007. Giving-up density and dietary shifts in the white-footed mouse, *Peromyscus leucopus*. Ecology 88:87–95.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution 17:170–176.

Sikes, R. S., W. L. Gannon, and The Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of mammalogy 92:235–253.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Simley, J. D., and W. J. Carswell, Jr. 2009. The national map—hydrography. Fact sheet 2009-3054.1-4. U.S. Geological Survey, Reston, Virginia, USA.

Skinner, M., B. L. Parker, S. Gouli, and T. Ashikaga. 2003. Regional responses of hemlock woolly adelgid (Homoptera: Adelgidae) to low temperatures. Environmental Entomology 32:523–528.

Smith, M., M. Palmer, and A. Brenner. 2006. Landcover development: State/federal collaboration improves data quality, saves money. Earth Imaging Journal 3:16–19.

Smith, S. E., and D. J. Read. 1997. Mycorrhizal symbiosis. 2nd edition. Academic Press,

London, UK.

Snyder, D. P. 1982. *Tamias striatus*. Mammalian Species 53:1–8.

Stange, E. E., M. P. Ayres, and J. A. Bess. 2011. Concordant population dynamics of Lepidoptera herbivores in a forest ecosystem. Ecography 34:772–779.

Stapp, P., and G. A. Polis. 2003. Influence of pulsed resources and marine subsidies on insular rodent populations. Oikos 102:111–123.

Stephens, R. B., and E. M. Anderson. 2014. Habitat associations and assemblages of small mammals in natural plant communities of Wisconsin. Journal of Mammalogy 95:404–420.

Stephens, R. B., E. M. Anderson, S. R. Wendt, and J. K. Meece. 2014. Field identification of sympatric *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in Wisconsin from external measurements. The American Midland Naturalist 171:139–146.

Stephens, R. B., D. J. Hocking, M. Yamasaki, and R. J. Rowe. 2017a. Synchrony in small mammal community dynamics across a forested landscape. Ecography 40:1198–1209.

Stephens, R. B., T. J. Remick, M. J. Ducey, and R. J. Rowe. 2017b. Drivers of truffle biomass, community composition, and richness among forest types in the northeastern US. Fungal Ecology 29:30–41.

Stevens, R. D., and J. S. Tello. 2009. Micro-and macrohabitat associations in Mojave Desert rodent communities. Journal of Mammalogy 90:388–403.

Stock, B. C., and B. X. Semmens. 2013. MixSIAR GUI user manual: version 3.1. http://conserver. iugo-cafe. org/user/brice. semmens/MixSIAR.

Supp, S. R., and S. K. M. Ernest. 2014. Species-level and community-level responses to disturbance: a cross-community analysis. Ecology 95:1717–1723.

Svanbäck, R., and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society of London B: Biological Sciences 274:839–844.

Syväranta, J., A. Lensu, T. J. Marjomäki, S. Oksanen, and R. I. Jones. 2013. An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data. PloS one 8:e56094.

Tabacaru, C. A., J. S. Millar, and F. J. Longstaffe. 2011. Seasonal moulting in deer mice (*Peromyscus maniculatus*) in the Rocky Mountains, Alberta. Canadian Field-Naturalist 125:126–131.

Teron, J. N., and L. J. Hutchison. 2013. Consumption of truffles and other fungi by the American red squirrel (*Tamiasciurus hudsonicus*) and the eastern chipmunk (*Tamias striatus*) (Sciuridae) in northwestern Ontario. Canadian Field-Naturalist 127:57–59.

Terwilliger, J., and J. Pastor. 1999. Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. Oikos 85:83–94.

Thibault, K. M., and J. H. Brown. 2008. Impact of an extreme climatic event on community assembly. Proceedings of the National Academy of Sciences 105:3410–3415.

Thiers, H. D. 1984. The secotoid syndrome. Mycologia 76:1–8.

Thompson, I. D., and P. W. Colgan. 1987. Numerical responses of martens to a food shortage in northcentral Ontario. Journal of Wildlife Management 51:824–835.

Tóth, B. B., and Z. Barta. 2010. Ecological studies of ectomycorrhizal fungi: An analysis of survey methods. Fungal Diversity 45:3–19.

Trappe, J. 1988. Lessons from Alpine Fungi. Mycologia 80:1–10.

Trappe, J. M. 1979. The orders, families, and genera ofhypogeous Ascomycotina (truffles and their relatives). Mycotaxon 9:297–340.

Trappe, M., F. Evans, and J. M. Trappe. 2007. Field guide to North American truffles. Ten Speed Press, Berkeley, CA.

Urban, M. C., M. A. Leibold, P. Amarasekare, L. De Meester, R. Gomulkiewicz, M. E. Hochberg, C. A. Klausmeier, N. Loeuille, C. De Mazancourt, J. Norberg, and others. 2008. The evolutionary ecology of metacommunities. Trends in Ecology & Evolution 23:311–317.

Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307–3315.

Vasseur, D. A., and J. W. Fox. 2007. Environmental fluctuations can stabilize food web dynamics by increasing synchrony. Ecology Letters 10:1066–1074.

Vázquez, D. P., C. J. Melián, N. M. Williams, N. Blüthgen, B. R. Krasnov, and R. Poulin. 2007. Species abundance and asymmetric interaction strength in ecological networks. Oikos 116:1120–1127.

Vendettuoli, J. F., D. A. Orwig, J. A. Krumins, M. D. Waterhouse, and E. L. Preisser. 2015. Hemlock woolly adelgid alters fine root bacterial abundance and mycorrhizal associations in eastern hemlock. Forest Ecology and Management 339:112–116.

Vernes, K., S. Blois, and F. Bärlocher. 2004. Seasonal and yearly changes in consumption of hypogeous fungi by northern flying squirrels and red squirrels in old-growth forest, New Brunswick. Canadian Journal of Zoology 82:110–117.

Vernes, K., M. Castellano, and C. N. Johnson. 2001. Effects of season and fire on the diversity of hypogeous fungi consumed by a tropical mycophagous marsupial. Journal of Animal Ecology 70:945–954.

Vernes, K., T. Cooper, and S. Green. 2015. Seasonal fungal diets of small mammals in an Australian temperate forest ecosystem. Fungal Ecology 18:107–114.

Wagner, S., C. Collet, P. Madsen, T. Nakashizuka, R. D. Nyland, and K. Sagheb-Talebi. 2010. Beech regeneration research: from ecological to silvicultural aspects. Forest Ecology and

Management 259:2172–2182.

Vander Wall, S. B. 2010. How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:989–997.

Wells, K., H. Feldhaar, and R. B. O'Hara. 2014. Population fluctuations affect inference in ecological networks of multi-species interactions. Oikos 123:589–598.

Welsh, C. J. E., and W. M. Healy. 1993. Effect of even-aged timber management on bird species diversity and composition in northern hardwoods of New Hampshire. Wildlife Society Bulletin 21:143–154.

Winfree, R., J. W Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecology Letters 18:626–635.

Wolff, J. O. 1985. The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *Peromyscus maniculatus*. Canadian Journal of Zoology 63:2657–2662.

Wolff, J. O. 1996a. Coexistence of white-footed mice and deer mice may be mediated by fluctuating environmental conditions. Oecologia 108:529–533.

Wolff, J. O. 1996b. Population fluctuations of mast-eating rodents are correlated with production of acorns. Journal of Mammalogy 77:850–856.

Wolff, J. O., R. D. Dueser, and K. S. Berry. 1985. Food habits of sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*. Journal of Mammalogy 66:795–798.

Wrazen, J. A., and G. E. Svendsen. 1978. Feeding ecology of a population of eastern chipmunks (*Tamias striatus*) in southeast Ohio. American Midland Naturalist 100:190–201.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Yates, T. L., J. N. Mills, C. A. Parmenter, T. G. Ksiazek, R. R. Parmenter, J. R. Vande Castle, C. H. Calisher, S. T. Nichol, K. D. Abbott, J. C. Young, M. L. Morrison, B. J. Beaty, J. L. Dunnum, R. J. Baker, J. Salazar-Bravo, and C. J. Peters. 2002. The ecology and evolutionary history of an emergent disease: Hantavirus Pulmonary Syndrome. Bioscience 52:989–998.

Yerger, R. W. 1953. Home range, territoriality and populations of the chipmunk in central New York. Journal of Mammalogy 34:448–458.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

APPENDIX A

IACUC Approval for use of Animals in Research

University *of* New Hampshire

Research Integrity Services, Service Building
51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

27-Aug-2012

Rowe, Rebecca J
Natural Resources & the Environment, James Hall Rm 114
Durham, NH 03824

IACUC #: 120708
Project: Species Vulnerability to Environmental Change: Insights from Land-Use Legacies
Category: D
Approval Date: 22-Aug-2012

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used.*

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:
1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. Information about the program, including forms, is available at http://unh.edu/research/occupational-health-program-animal-handlers.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Jill A. McGaughy, Ph.D.
Chair

cc: File

University *of* New Hampshire

Research Integrity Services, Service Building
51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

01-Apr-2014

Rowe, Rebecca J
Natural Resources & the Environment, James Hall Rm 136
Durham, NH 03824

IACUC #: 140304
Project: Abiotic and Biotic Drivers of Small Mammal Community Structure in the White Mountain National Forest
Category: D
Approval Date: 21-Mar-2014

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used.* The IACUC made the following comment(s) on this protocol:

1. All principal investigators/instructors are responsible for knowing about zoonotic diseases, safety issues, laws, and regulations applicable to the proposed field study activity, taking appropriate precautions, instructing/informing project personnel and students ahead of time about pertinent issues accordingly, and ensuring project personnel review the collection permit before capturing/trapping/handling any animals. Please contact the UNH Office of Environmental Health & Safety (603/862-4041) with any questions.
2. The investigator is responsible for obtaining any necessary permits for capturing animals as proposed in the study.

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:
1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. Information about the program, including forms, is available at http://unh.edu/research/occupational-health-program-animal-handlers.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Jill A. McGaughy, Ph.D.
Chair

cc: File

APPENDIX B

Supplementary Figures for Chapter 1

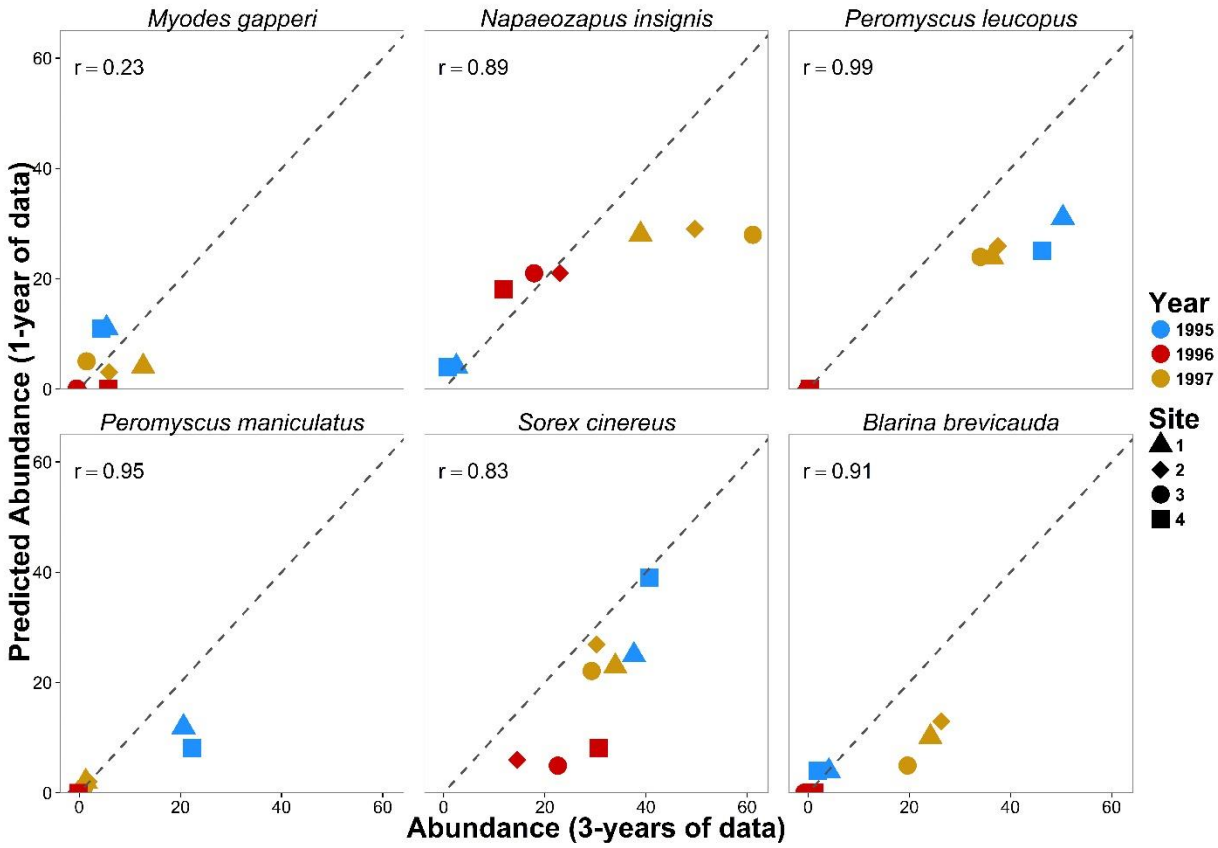


Figure B1. Comparison of abundance and predicted abundance for the six most common small mammal species at four sites in Bartlett Experimental Forest during three years of trapping. Abundance data were derived using count data collected during trapping and were adjusted for imperfect detection using a hierarchical open population model within a Bayesian framework. In a separate model, abundance data from 1-year (randomly drawn) were used to estimate abundance for two years (comparison for the third year not shown). Count data for modeling predicted abundance came from 1995 (sites 3 and 2), 1996 (site 1), and 1997 (site 4). Both models used landscape variables, detection variables, and the three years of data from White Mountain National Forest small mammal trapping to derive abundance values. Year trapped is indicated by color (1995 = blue, 1996 = red, and 1997 = yellow). Sites are denoted by various shapes. Dashed line represents line of equality.

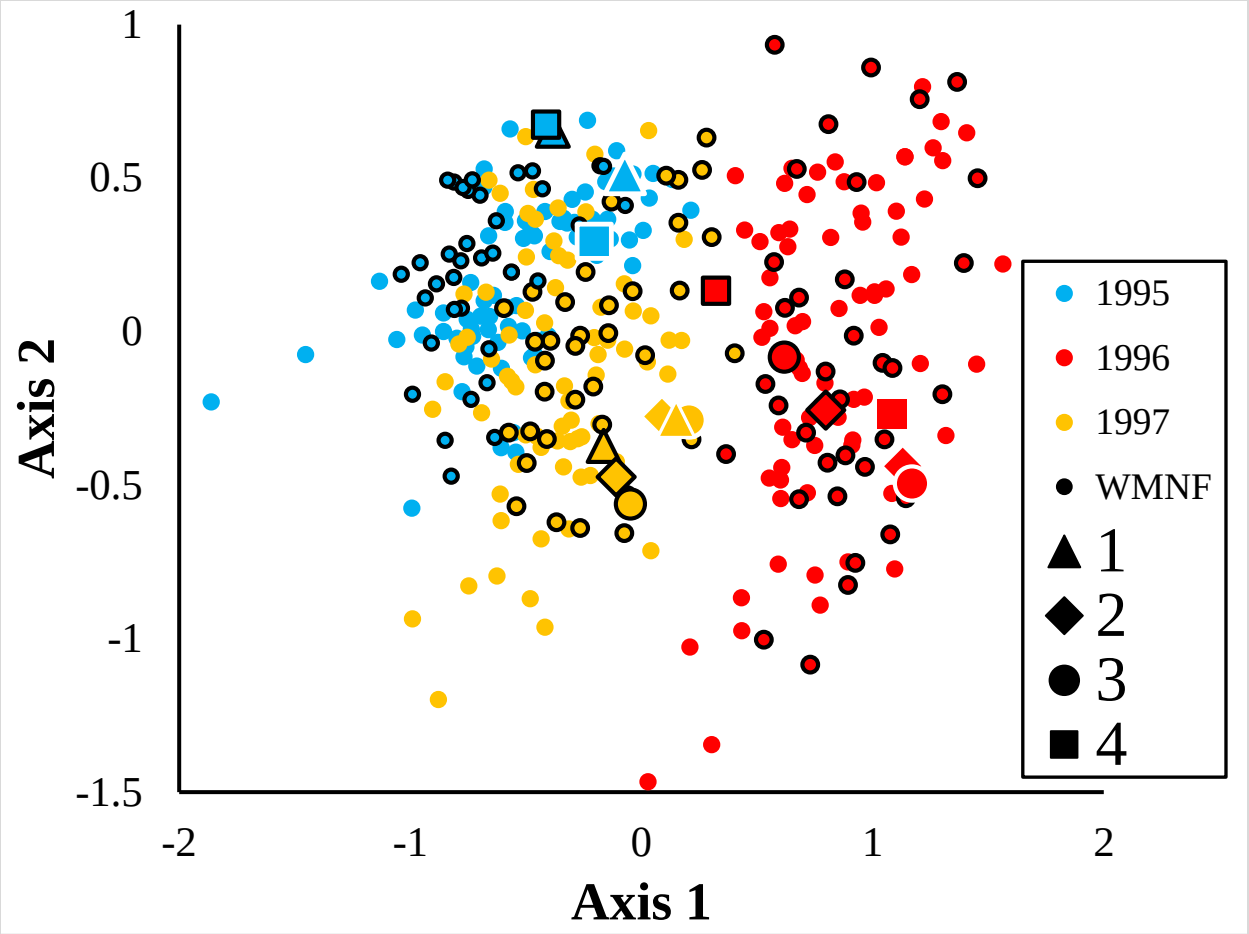


Figure B2. Nonmetric multidimensional scaling ordination of White Mountain National Forest (WMNF) and Bartlett Experimental Forest (BEF) small mammal communities in 2-dimensional space. Outlined shapes represent communities composed of abundance data from sites which were trapped in that year, whereas shapes without an outline represent communities composed of model predicted species abundance data (i.e., sites were not trapped in that year and species abundance data were predicted based on landscape variables, detection variables, count data from other sites trapped during that year, and count data from the year it was trapped). Year is indicated by color (1995 = blue, 1996 = red, and 1997 = yellow). WMNF sites used in analyses of this manuscript are denoted by small circles and BEF data (used as validation) are denoted by various large shapes. Increased pairwise distance between sites (shapes) indicates decreased similarity (Bray Curtis) of community composition. Note that this analysis is a separate ordination from the one in the main text (Fig. 1.5), and thus has a slightly different ordination structure.

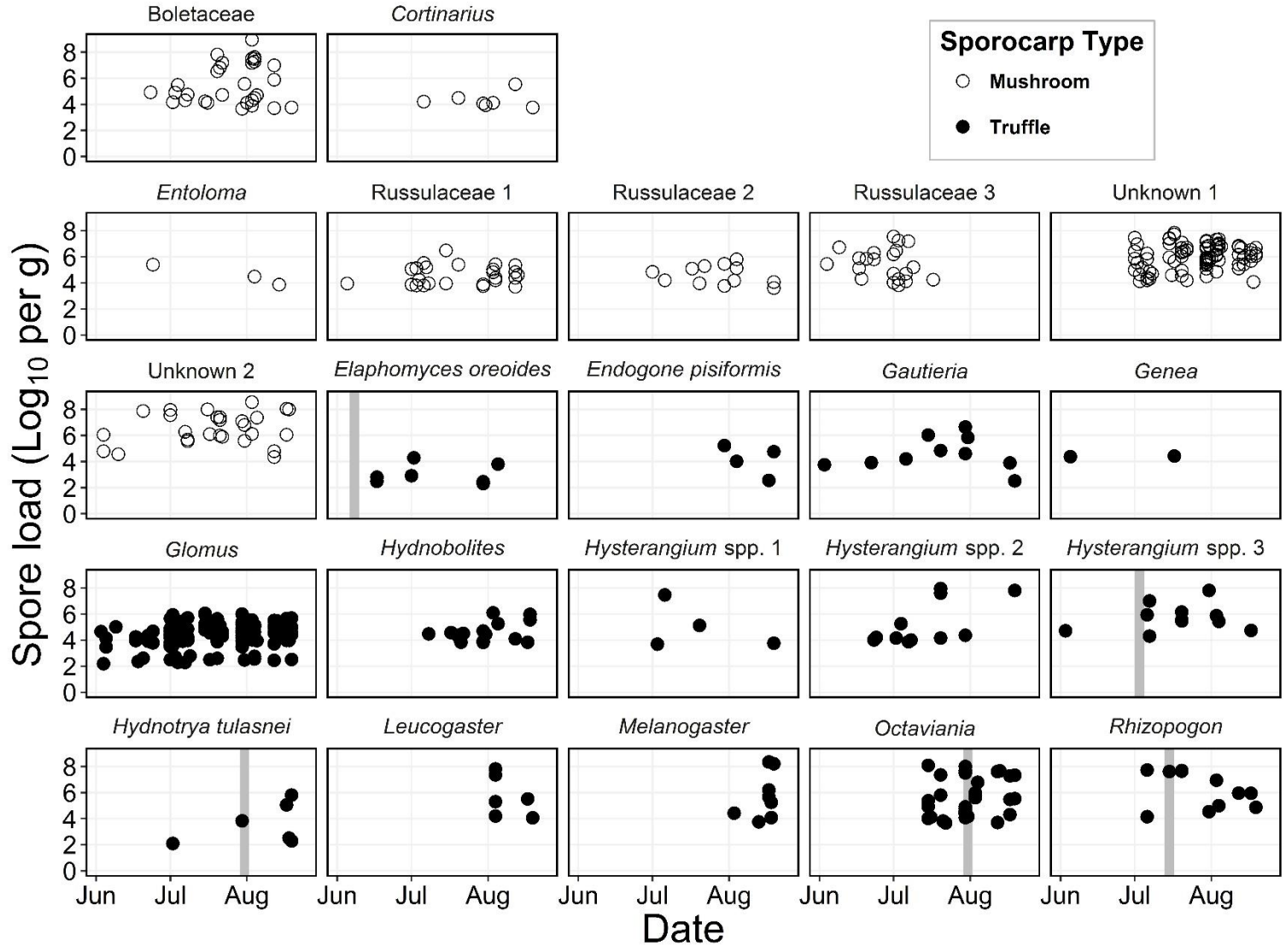
APPENDIX C

Supplementary Tables and Figures for Chapter 2

Table C1. Summary statistics of grid level environmental variables and results of an *envfit* analysis comparing the correlation between environmental variables and truffle community composition. Significant ($\alpha = 0.05$) correlations of the *envfit* are shown in bold.

Environmental variables	Summary statistics		*envfit*	
	Mean	Range	r^2	*P*
Eastern hemlock - Basal area (m^2/ha)	16.41	(0.90 - 34.85)	0.6095	**0.001**
American beech - Basal area (m^2/ha)	5.82	(0.75 - 18.22)	0.4824	**0.001**
Leaf litter depth (cm)	2.51	(1.77 - 3.38)	0.4365	**0.001**
Red spruce - Basal area (m^2/ha)	3.80	(0.00 - 12.78)	0.2819	**0.003**
Red maple - Basal area (m^2/ha)	10.25	(1.10 - 17.36)	0.1955	**0.009**
White ash - Basal area (m^2/ha)	1.61	(0.00 - 4.82)	0.1887	**0.012**
Volume DWD (m^3/ha)	62.83	(47.64 - 77.91)	0.0549	0.297
Yellow birch - Basal area (m^2/ha)	1.84	(0.58 - 3.00)	0.0287	0.554
Sampling day (Day of the year)	214.65	(158 - 278)	0.0228	0.581

Figure C1. Spore abundance (log_{10}) of mushroom and truffle taxa (excluding the most common species shown in Fig. 2.2) found in scat samples of eastern chipmunks. Vertical gray bars represent the time in which the truffle species was detected during field surveys. Most mushroom taxa could only be identified to family and most truffle taxa to genus.



APPENDIX D

Supplementary Materials for Chapter 3

Seasonal hair bins

Hair is metabolically inert and integrates an isotopic signature of diet at the time of growth. Thus, because *Peromyscus* only molt at certain times of the year (See *Stable Isotope integration period and values* section in manuscript), the window of hair dietary assimilation may be offset from the time of collection. To correctly match hair samples to their time of growth, we constructed two seasonal bins corresponding with the summer season (11 week period from May 15 to August 7) and the fall season (11 week period from August 8 to October 31). These seasonal isotopic integration bins start approximately two weeks prior to when trapping began to account for hair from individuals captured at the start of sampling (Gottschang 1956). The summer season included hair samples collected from young of the year between June 1 and August 19 (last day of summer sampling) and hair samples collected from adults between July 2 and August 19. The fall season included hair samples from all individuals collected between September 12 (first day of fall sampling) and October 31. Hair samples from adults captured between June 1 and July 1 (prior to summer molt) were assigned to the fall season of the prior year. Several hair samples did not fall within these designations and were adjusted accordingly. These included 10 adults captured between July 2 and July 9 that had not gone

through a summer molt and were included with the fall season of the prior year. Additionally, 8 individuals in the process of entering adult pelage collected after August 12 were included in the fall season of that year. For young of the year, with two hair samples collected during the same seasonal bin (from sub-adult and adult pelage during the summer), we randomly selected one of the samples to include in analyses. We excluded hair samples from juveniles (≤ 9 g) because these samples likely reflect their mother's milk rather than freely consumed food sources (Miller et al. 2011).

LITERATURE CITED

Gottschang, J. L. 1956. Juvenile molt in *Peromyscus leucopus noveboracensis*. Journal of Mammalogy 37:516–520.

Miller, J. F., J. S. Millar, and F. J. Longstaffe. 2011. Stable nitrogen and carbon isotope discrimination between juveniles and adults in an income-breeding small mammal (*Peromyscus maniculatus*). Mammalian Biology 76:563–569.

APPENDIX E

Supplementary Material, Tables, and Figures for Chapter 4

Stable isotope analysis

For each rodent species, we used stable isotope analysis of dietary food sources and rodent hair, coupled with Bayesian mixing models, to determine the proportion of the diet composed of fungi. Our analyses were restricted to hair collected from July through August of 2014.

Food sources

For isotopic analysis of the resource base, we collected six potential food sources known to comprise the majority of dietary items of the rodent species: beech nuts, red maple seeds, ectomycorrhizal (EM) fungal sporocarps, arbuscular mycorrhizal (AM) fungal sporocarps, berries, and arthropods (Linzey and Linzey 1973, DeGraaf and Yamasaki 2001). Beech nuts, red maple seeds, and berries (hobblebush and partridge berries [*Mitchella repens*]) were collected opportunistically while trapping. Arthropods were collected using small pitfall traps and were analyzed at the order level: beetles (Coleoptera), grasshoppers (Orthoptera) and spiders (Araneae). The EM sporocarps (genus *Elaphomyces*) were collected as part of a companion study (Stephens et al. 2017) and AM sporocarps (primarily *Glomus* spp.) were taken from

stomachs of woodland jumping mice (*Napaeozapus insignis;* > 70% fungi by volume) because they are too small to be detected with field surveys (Stephens et al. 2017). *Napaeozapus insignis* were collected at Bartlett Experimental Forest during the summer of 2015 by the US Forest Service (USFS). Individual samples within a food source were collected at the grid level to form a composite sample, with the exception of EM and AM fungi for which samples were analyzed individually.

Stable Isotope Measurement

Hair samples were soaked in 2:1 chloroform:methanol for 24 hours to remove surface oils, after which they were re-rinsed, air dried, and cut into small pieces. Food items were rinsed with 2:1 chloroform:methanol and ground to a fine powder. Hair samples (1 mg) and food items (1 – 5 mg) were weighed into tin capsules and analyzed for stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes and elemental composition (%C, %N) at the University of New Hampshire Stable Isotope Lab using an Elementar Americas Pyrocube elemental analyzer coupled to a GeoVision isotope ratio mass spectrometer. Raw $\delta^{13}C$ and $\delta^{15}N$ values were adjusted based on a 3-point normalization using in-house standards. Isotopes are expressed in delta (δ) notation as parts per thousand (‰) deviation from the standard using the formula:

$$\delta = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, and standards are Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric N_2 ($\delta^{15}N$). Measurement precision based on repeated analyses of in-house standards was ± 0.1 ‰ for $\delta^{13}C$ and ± 0.2 ‰ for $\delta^{15}N$. To capture an isotopic signal from the general population and avoid an individual grid from biasing our results, we used up to nine hair samples

per species from a grid. In total we analyzed hair samples from 52 *Myodes gapperi*, 41 *N. insignis*, 88 *T. striatus*, 63 *Peromyscus maniculatus*, and 58 *P. leucopus*.

Dietary Composition

We assessed the contribution of fungi to the diets of rodents using Bayesian stable isotope mixing models in the R package 'MixSIAR' (Stock and Semmens 2013). *MixSIAR* uses $\delta^{15}N$ and $\delta^{13}C$ values from both consumer tissues (i.e., hair) and each food source along with discrimination factors, elemental concentrations, and the uncertainties surrounding those values to calculate the relative proportion of food sources consumed. We used separate models for each species; running each model with three chains for 200,000 iterations, removing the first 50,000 and thinning by 50, resulting in 9,000 draws of the posterior distribution. The proportion of fungi in the diets of rodents was calculated as the contribution of both EM and AM fungi.

For all mixing models we used informative priors which improve precision and accuracy (Moore and Semmens 2008). Informative priors were given the same weight as an uninformative prior, but the contribution of individual food sources was scaled by the relative proportion of the number of weeks it was available during a season (See Fig. 3.2 in Chapter 3). Temporal availability was based on phenology recorded in the literature, food sources observed in the field, and through microscopy of scat. Hair samples were collected during a beech masting year (2014, Chapter 3) and we considered beech nuts to be available during the entire summer season. Red maple seeds are available during late spring through early summer (Houle 1994), with most seeds removed within 1 - 2 months (Myster and Pickett 1993). EM sporocarps (Stephens et al. 2017), berries (Gervais and Wheelwright 1994), and arthropods are available year round, whereas AM sporocarps are primarily consumed during summer. For the food source parameters

of $\delta^{15}N$ and $\delta^{13}C$, we used means and standard deviations of collected food items and accounted for differences in elemental concentrations.

Consumer tissues are enriched in ^{13}C and ^{15}N relative to food sources and to put them into consumer isospace they must be adjusted. Although discrimination factors have been derived experimentally for both *P. leucopus*, (DeMots et al. 2010), *P. maniculatus* (Miller et al. 2008), and *M. gapperi* (Sare et al. 2005), applying these values to our data caused hair samples to fall well outside the isospace occupied by food sources. Fractionation of both $\delta^{13}C$ and $\delta^{15}N$ can vary greatly by diet (Sare et al. 2005), and it is likely that lab derived discrimination factors do not reflect those of natural diets. Therefore, we focused on *P. maniculatus*, *N. insignis*, and *M. gapperi* to calculate isotopic enrichment factors for natural diets at Bartlett Experimental Forest using stomach contents (bulk diet) and hair samples collected from rodents during the summer of 2015. Our derived discrimination factor for *P. maniculatus* was also used for *P. leucopus* and *T. striatus* in mixing models as these species have similar diets (DeGraaf and Yamasaki 2001). To calculate discrimination factors we subtracted the average isotopic value (δ13C and δ15N) of stomach samples from the average isotopic values of hair samples. Samples sizes for stomachs were: *P. maniculatus* (n = 9), *N. insignis* (n =18), and *M. gapperi* (n = 20) and samples sizes for hair were: *P. maniculatus* (n = 11), *N. insignis* (n =20), and *M. gapperi* (n = 20). Derived discrimination factors were: *P. maniculatus* (1.92 for $\delta^{15}N$ and 4.64 for $\delta^{13}C$), *N. insignis* (1.99 for $\delta^{15}N$ and 4.82 for $\delta^{13}C$), and *M. gapperi* (0.52 for $\delta^{15}N$ and 4.27 for $\delta^{13}C$). We used large standard deviations of 1.0‰ for $\delta^{15}N$ and 2.0‰ for $\delta^{13}C$ to account for any uncertainty surrounding our discrimination factors.

LITERATURE CITED

DeGraaf, R. M., and M. Yamasaki. 2001. New England wildlife: habitat, natural history, and distribution. University Presss of New England, Hanover, New Hampshire, USA.

DeMots, R. L., J. M. Novak, K. F. Gaines, A. J. Gregor, C. S. Romanek, and D. A. Soluk. 2010. Tissue–diet discrimination factors and turnover of stable carbon and nitrogen isotopes in white-footed mice (*Peromyscus leucopus*). Canadian Journal of Zoology 88:961–967.

Gervais, J. A., and N. T. Wheelwright. 1994. Winter fruit removal in four plant species in Maine. Maine Naturalist 2:15–24.

Houle, G. 1994. Spatiotemporal patterns in the components of regeneration of four sympatric tree species--*Acer rubrum*, *A. saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*. Journal of Ecology 82:39–53.

Linzey, D. W., and A. V Linzey. 1973. Notes on food of small mammals from Great Smoky Mountains National Park, Tennessee-North Carolina. Journal of Elisha Mitchell Scientific Society 89:6–14.

Miller, J. F., J. S. Millar, and F. J. Longstaffe. 2008. Carbon- and nitrogen-isotope tissue-diet discrimination and turnover rates in deer mice, *Peromyscus maniculatus* 86:685–691.

Moore, J. W., and B. X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11:470–480.

Myster, R. W., and S. T. A. Pickett. 1993. Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. Oikos 66:381–388.

Sare, D. T. J., J. S. Millar, and F. J. Longstaffe. 2005. Tracing dietary protein in red-backed voles (*Clethrionomys gapperi*) using stable isotopes of nitrogen and carbon. Canadian Journal of Zoology 725:717–725.

Stephens, R. B., T. J. Remick, M. J. Ducey, and R. J. Rowe. 2017. Drivers of truffle biomass, community composition, and richness among forest types in the northeastern US. Fungal Ecology 29:30–41.

Stock, B. C., and B. X. Semmens. 2013. MixSIAR GUI user manual: version 3.1. http://conserver. iugo-cafe. org/user/brice. semmens/MixSIAR.

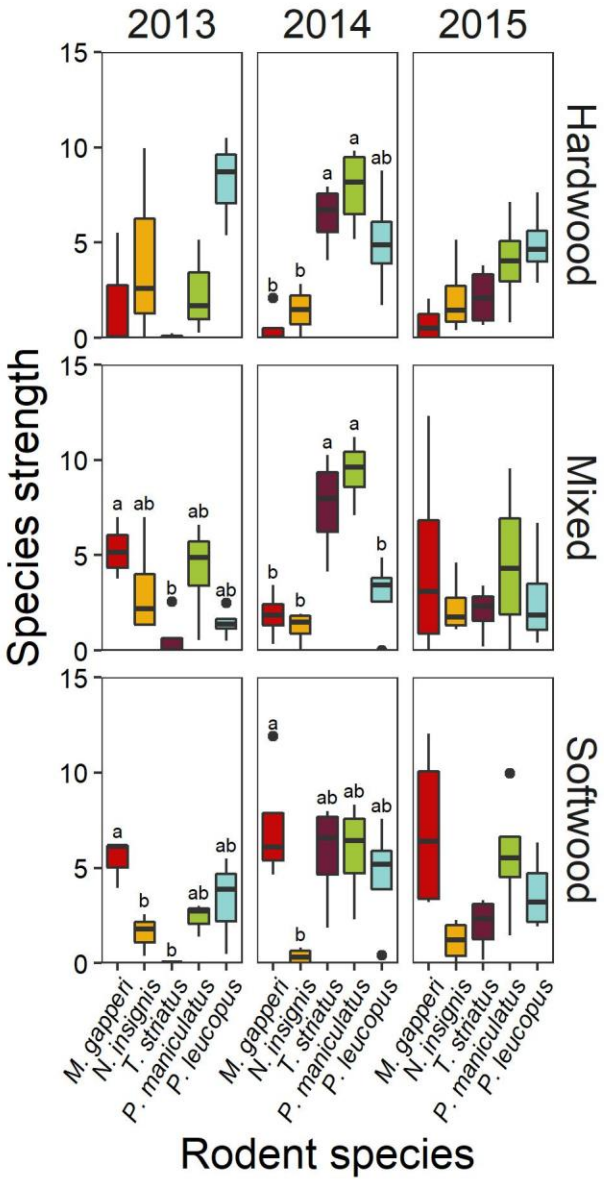


Figure E1. Boxplots indicating species strength of the five rodents in the incidence networks. Within a given year and forest type, letters above boxes indicate a significant ANOVA: 2013 Hardwood ($F_{4,10} = 2.88$; $P = 0.08$), 2014 Hardwood ($F_{4,15} = 10.67$; $P < 0.001$), 2015 Hardwood ($F_{4,15} = 3.00$; $P = 0.053$), 2013 Mixed ($F_{4,15} = 4.00$; $P = 0.021$), 2014 Mixed ($F_{4,15} = 15.77$; $P < 0.001$), 2015 Mixed ($F_{4,15} = 0.51$; $P = 0.732$), 2013 Softwood ($F_{4,10} = 6.02$; $P = 0.009$), 2014 Softwood ($F_{4,15} = 3.99$; $P = 0.021$), and 2014 Softwood ($F_{4,15} = 3.03$; $P = 0.05$). Rodents with the

same letters are not significantly different, whereas rodents with different letters are significantly different.

Table E1. Mixed effects models comparing the proportion of rodent-fungal interactions detected among years as indicated by the abundance-based richness estimator Chao 1. Tukey's post hoc tests among years indicated that the proportion of interaction detected did not differ. Random effects included a random intercept for grid within year to account for repeated measurements of grids among years. Mixed effects models were carried out using lme in the R-package 'nlme' and pairwise Tukey's post hoc tests were performed using 'emmeans' in the R-package 'emmeans'.

Model components	β	se	*P* value
Intercept (2013)	0.673	0.028	<0.001
2014	0.029	0.039	0.454
2015	-0.042	0.039	0.295

Table E2. Percentages of scat samples for each rodent species that contained spores from each fungal taxa. Total detections are shown parenthetically. Total scat samples examined were: *Myodes gapperi* (187), *Napaeozapus insignis* (166), *Tamias striatus* (173), *Peromyscus maniculatus* (402), and *Peromyscus leucopus* (275). G-test of goodness-of-fit was used to determine differences in distributions among rodent species are shown for the 12 most commonly detected fungal taxa. Among fungal taxa, letters denote significant differences among rodents as indicated by Bonferroni post hoc tests with the same letter indicating no significant differences and different letters indicate significant differences. Superscripts on fungal taxa denote fungal category: mycorrhizal (M), saprophytic (S), or unknown (U) and fruiting habitat: truffles that are sequestrate or hypogeous (T), mushrooms that are epigeous (E), and taxa that may be both (B).

Fungal taxa	Rodent species					G - test	
	M. gapperi	*N. insignis*	*T. striatus*	*P. maniculatus*	*P. leucopus*	G - test	*P* value
Glomus^{M,T}	96.3^{a} (180)	98.8^{a} (164)	78.6^{a} (136)	79.4^{a} (319)	66.9^{a} (184)	10.15	0.038
Elaphomyces verruculosus^{M,T}	63.1^{a} (118)	31.3^{b} (52)	54.3^{ab} (94)	39.3^{b} (158)	41.1^{ab} (113)	18.40	0.001
Elaphomyces macrosporus^{M,T}	36.9 (69)	40.4 (67)	50.9 (88)	42.0 (169)	41.1 (113)	3.07	0.546
Elaphomyces bartlettii^{M,T}	11.8^{bc} (22)	9.0^{bc} (15)	29.5^{a} (51)	21.6^{a} (87)	18.9^{abc} (52)	22.65	<0.001
Russulaceae 1^{M,E}	42.2^{a} (79)	10.8^{b} (18)	17.3^{b} (30)	10.9^{b} (44)	19.3^{b} (53)	51.40	<0.001
Unknown 1^{U,E}	34.2^{a} (64)	3.0^{b} (5)	52.6^{a} (91)	5.5^{b} (22)	10.2^{b} (28)	157.8	<0.001
Boletaceae 1^{M,E}	41.7^{a} (78)	3.6^{d} (6)	18.5^{b} (32)	8.7^{cd} (35)	14.5^{bc} (40)	79.38	<0.001
Russulaceae 3^{M,E}	5.9^{b} (11)	19.9^{ac} (33)	9.8^{bc} (17)	16.4^{ac} (66)	22.9^{a} (63)	25.70	<0.001
Hydnotrya cubispora^{M,T}	28.9^{a} (54)	12.0^{b} (20)	23.1^{a} (40)	7.0^{b} (28)	8.7^{b} (24)	48.12	<0.001
Elaphomyces americanus^{M,T}	3.7^{b} (7)	9.6^{ab} (16)	15.6^{a} (27)	11.9^{a} (48)	12.7a (35)	14.95	0.005
Octaviania^{M,T}	15.5^{a} (29)	2.4^{b} (4)	18.5^{a} (32)	4.5^{b} (18)	5.1^{b} (14)	43.52	<0.001
Cortinarius^{M,B}	19.8^{a} (37)	3.0^{bc} (5)	4.6^{bc} (8)	2.2^{c} (9)	7.6^{b} (21)	49.21	<0.001
Unknown 2^{U,E}	0.5 (1)	1.8 (3)	13.9 (24)	5.0 (20)	6.2 (17)		
Russulaceae 2^{M,E}	3.7 (7)	1.8 (3)	7.5 (13)	3.5 (14)	6.9 (19)		
Elaphomyces oreoides^{M,T}	0.5 (1)	4.2 (7)	5.8 (10)	3.7 (15)	8.0 (22)		
Gauteria^{M,T}	7.0 (13)	0.6 (1)	5.8 (10)	5.0 (20)	2.2 (6)		
Endogone pisiformis^{S,T}	0.5 (1)	1.2 (2)	2.3 (4)	7.2 (29)	4.0 (11)		
Hydnobolites^{M,T}	0.0 (0)	0.6 (1)	9.8 (17)	5.5 (22)	1.5 (4)		
Rhizopogon^{M,T}	11.2 (21)	1.2 (2)	6.4 (11)	1.0 (4)	0.4 (1)		

Boletaceae 2[M,E]	10.2 (19)	0.0 (0)	1.7 (3)	2.2 (9)	1.5 (4)
Entoloma[M,E]	5.3 (10)	1.2 (2)	1.2 (2)	2.2 (9)	4.0 (11)
Hydnotrya tulasnei[M,T]	2.1 (4)	3.0 (5)	4.6 (8)	2.5 (10)	0.4 (1)
Hysterangium spp. 3[M,T]	3.7 (7)	0.0 (0)	6.9 (12)	1.5 (6)	1.1 (3)
Leucogaster[M,T]	2.1 (4)	1.2 (2)	4.6 (8)	1.7 (7)	2.5 (7)
Melanogaster[M,T]	1.1 (2)	3.6 (6)	5.8 (10)	1.2 (5)	0.7 (2)
Tuber[M,T]	2.1 (4)	0.0 (0)	1.2 (2)	3.2 (13)	1.5 (4)
Hysterangium spp. 2[M,T]	2.7 (5)	0.0 (0)	6.9 (12)	0.2 (1)	1.1 (3)
Genea[M,T]	1.1 (2)	1.2 (2)	0.6 (1)	1.5 (6)	1.1 (3)
Gymnomyces[M,T]	3.2 (6)	0.0 (0)	0.0 (0)	0.7 (3)	0.0 (0)
Leucophleps[M,T]	1.1 (2)	0.0 (0)	0.0 (0)	0.2 (1)	1.5 (4)
Hymenogaster[M,T]	0.5 (1)	1.8 (3)	0.0 (0)	0.5 (2)	0.0 (0)
Hysterangium spp. 1[M,T]	0.0 (0)	0.6 (1)	2.3 (4)	0.0 (0)	0.4 (1)
Chamonixia[M,T]	0.5 (1)	0.0 (0)	0.6 (1)	0.0 (0)	0.0 (0)
Elaphomyces remickii[M,T]	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.4 (1)

Table E3. Results of mixed effects models predicting richness and diversity of spores in the scat of five rodent species. Random effects included a random intercept for grid within year.

Model Components	Richness		Diversity	
	β (se)	*P* value	β (se)	*P* value
Intercept (*M. gapperi*)	4.55 (0.14)	<0.001	0.69 (0.03)	<0.001
N. insignis	-1.76 (0.17)	<0.001	-0.44 (0.04)	<0.001
P. leucopus	-1.42 (0.15)	<0.001	-0.27 (0.04)	<0.001
P. maniculatus	-1.59 (0.14)	<0.001	-0.31 (0.03)	<0.001
T. striatus	0.02 (0.17)	0.899	-0.11 (0.04)	0.005

Table E4. Mean and standard error of spore loads (millions per g of scat) carried by rodent species. Fungal taxa are arranged in descending order from the most to least detected. Kruskal-Wallis tests were used to test for differences among rodent species. Rodents with the same letter are not significantly different whereas different letters indicate significant differences. Among fungal taxa, letters denote significant differences as indicated by Bonferroni post hoc tests.

Fungal taxa	Rodent species					Kruskal-Wallis test	
	M. gapperi	*N. insignis*	*T. striatus*	*P. maniculatus*	*P. leucopus*	χ^2	*P* value
Glomus	0.210^{b} (0.021)	0.696^{a} (0.053)	0.088^{cd} (0.015)	0.150^{c} (0.014)	0.140^{d} (0.024)	265.7	<0.001
Elaphomyces verruculosus	0.257^{a} (0.089)	0.002^{c} (0.001)	0.007^{b} (0.002)	0.004^{c} (0.002)	0.006^{bc} (0.006)	79.0	<0.001
Elaphomyces macrosporus	0.120 (0.061)	0.374 (0.210)	0.031 (0.016)	0.077 (0.028)	0.082 (0.050)	3.5	0.480
Elaphomyces bartlettii	0.130^{a} (0.208)	0.047^{ab} (0.073)	0.081^{c} (0.131)	0.119^{c} (0.078)	0.124^{abc} (0.117)	26.9	<0.001
Russulaceae 1	2.146^{a} (0.771)	0.034^{b} (0.055)	0.036^{b} (0.045)	0.019^{b} (0.021)	0.027^{b} (0.014)	113.3	<0.001
Unknown 1	1.531^{a} (0.591)	0.002^{b} (0.009)	2.887^{a} (0.848)	0.127^{a} (0.515)	0.132^{a} (0.193)	277.8	<0.001
Boletaceae 1	7.147^{a} (2.647)	0.001^{c} (0.003)	6.882^{b} (12.363)	0.003^{c} (0.004)	0.016^{bc} (0.026)	154.0	<0.001
Russulaceae 3	0.049^{b} (0.151)	0.929^{ac} (0.612)	0.448^{bc} (0.791)	1.005^{ac} (1.277)	1.306^{a} (0.633)	32.7	<0.001
Hydnotrya cubispora	0.186^{a} (0.087)	0.022^{b} (0.037)	0.105^{a} (0.099)	0.008^{b} (0.017)	0.011^{b} (0.023)	76.8	<0.001
Elaphomyces americanus	0.001^{b} (0.007)	0.008^{ab} (0.023)	0.001^{a} (0.000)	0.012^{a} (0.024)	0.001^{a} (0.001)	14.2	0.007
Octaviania	1.805^{a} (1.668)	$<0.001^{b}$ (0.001)	2.685^{a} (2.429)	0.006^{b} (0.023)	0.023^{b} (0.098)	59.8	<0.001
Cortinarius	1.037^{a} (0.776)	0.015^{b} (0.064)	0.003^{b} (0.009)	0.014^{b} (0.070)	0.025^{b} (0.081)	73.9	<0.001

Table E5. Results from the mixed effects models predicting abundance of five rodent species among years and forest types. Fixed effects included year, forest type, and the interaction between year and forest type. For each variable, the effect of a variable is relative to the one not listed (e.g., effect of 2014 is relative to 2013). Random effects included a random intercept for grid within year to account for repeated measurements among years.

Model Components	*M. gapperi*		*N. insignis*		*T. striatus*		*P. maniculatus*		*P. leucopus*	
	β (se)	*P* value	β (se)	*P* value	β (se)	P value	β (se)	P value	β (se)	P value
Intercept	1.25 (2.06)	0.551	10.50 (5.01)	0.051	0.25 (1.21)	0.838	4.00 (5.92)	0.508	9.00 (1.88)	<0.001
2014	-0.25 (2.69)	0.927	-5.25 (4.09)	0.215	7.75 (1.71)	<0.001	33.00 (6.74)	<0.001	-0.75 (2.12)	0.728
2015	-0.75 (2.69)	0.784	1.75 (4.09)	0.674	1.50 (1.71)	0.391	6.75 (6.74)	0.33	-0.00 (2.12)	1.000
Mixed	4.25 (2.91)	0.178	-1.25 (7.09)	0.864	-0.00 (1.71)	1.000	2.00 (8.37)	0.817	-5.75 (2.66)	0.059
Softwood	2.00 (2.91)	0.509	-8.75 (7.09)	0.248	-0.25 (1.71)	0.887	-0.25 (8.37)	0.977	-5.00 (2.66)	0.093
2014*Mixed	-0.25 (3.81)	0.948	2.75 (5.78)	0.64	1.75 (2.41)	0.478	-13.25 (9.53)	0.181	4.00 (3.00)	0.200
2015*Mixed	2.00 (3.81)	0.606	-7.00 (5.78)	0.242	<0.01 (2.41)	1.000	-7.75 (9.53)	0.427	0.75 (3.00)	0.806
2014*Softwood	7.00 (3.81)	0.083	4.75 (5.78)	0.422	0.50 (2.41)	0.838	-13.00 (9.53)	0.189	7.00 (3.00)	0.032
2015*Softwood	7.00 (3.81)	0.083	-0.25 (5.78)	0.966	1.75 (2.41)	0.478	2.50 (9.53)	0.796	2.00 (3.00)	0.514

Table E6. Results from mixed effects models for network level metrics among years and network types. Fixed effects variables included year, network type, and the interaction between year and network type. For each variable, the effect of a variable is relative to the one not listed (e.g., effect of 2014 is relative to 2013). Random effects included a random intercept for grid within year to account for repeated measurements among years.

Model Components	Evenness		Generality (Fungi)		Specialization (H_2')	
	β (se)	P value	β (se)	*P* value	β (se)	*P* value
Intercept	0.77 (0.01)	<0.001	8.05 (0.66)	<0.001	0.65 (0.02)	<0.001
2014	0.05 (0.01)	0.002	4.63 (0.89)	<0.001	-0.14 (0.03)	<0.001
2015	<0.01 (<0.01)	0.905	0.76 (0.89)	0.402	-0.05 (0.03)	0.092
Disperser importance	-0.06 (0.01)	<0.001	-1.19 (0.36)	0.003	0.21 (0.02)	<0.001
2014*Disperser importance	-0.01 (0.01)	0.114	-1.88 (0.49)	<0.001	0.06 (0.03)	0.033
2015*Disperser importance	-0.01 (0.01)	0.446	-0.56 (0.49)	0.262	0.02 (0.03)	0.387